

ANATOMY OF HEAD AND NECK IN THE  
HUIA (*HETERALOCHA ACUTIROSTRIS*) WITH  
COMPARATIVE NOTES ON OTHER CALLAEIDAE

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# ANATOMY OF HEAD AND NECK IN THE HUIA (*HETERALOCHA ACUTIROSTRIS*) WITH COMPARATIVE NOTES ON OTHER CALLAEIDAE

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## SYNOPSIS

Spirit specimens and skeletons of the Huia (*Heteralocha acutirostris*) have been used in a detailed study of feeding adaptations in this extinct species. The Huia showed remarkable sexual dimorphism in bill form, and particular attention is paid throughout to differences between male and female. Comparison is made with the other members of the Callaeidae – *Creadion carunculatus* and *Callaeas cinevea*. The features studied indicate that the Huia was highly specialized for feeding by 'gaping' in decayed timber, in order to gain access to beetle grubs. The full extent of sexual dimorphism revealed by this study is reviewed, and its significance is discussed.

## I. INTRODUCTION

THE extinct Huia (*Heteralocha acutirostris*) of New Zealand is frequently quoted as an example of extreme sexual dimorphism among birds. This dimorphism is shown most conspicuously by the bill, which in the male was typically fairly straight, moderately long, and tapered evenly to a point; while in the female it was much longer, more slender, and strongly downcurved. There is little information on the extent of dimorphism beyond this. Phillipps (1963) mentions plumage differences and a tendency towards stronger claws in older males, and Selander (1966) gives bill, wing and tarsus measurements for a small sample of each sex. The anatomical study of the Huia by Garrod (1872) concentrated principally on establishing the affinities of the species, and did not inquire closely into its sexual dimorphism. The problem of its relationships is still not fully resolved beyond the fact that the Huia is closely related to two other New Zealand species – the Saddleback (*Creadion*

*carunculatus*) and the Kokako (*Callaeas cinerea*) (Stonor, 1942). The three together form the family *Callaeidae*, placed between the *Dicruridae* and *Grallinidae* by Mayr and Greenway (1956); close affinity with the *Sturnidae* has been suggested in the past (Garrod, 1872; Gray, 1870).

The present investigation has been concerned with the anatomical basis of the Huia's feeding specializations. In particular, I have attempted to discover the full extent of sexual dimorphism in feeding structures, and to correlate this where possible with bill form and feeding methods. It is thus a study of adaptation, unusual in that the principal forms to be compared are the two sexes of a single species. The material on which the investigation is based is contained in the avian anatomical collections of the British Museum (Natural History). These consist of six spirit and one osteological specimens of the Huia, one spirit specimen of the Saddleback and four spirit specimens of the Kokako. It is thought that the Huia spirit specimens may be the only fluid-preserved examples of this species in existence, although there is at least one skeleton in New Zealand (Phillipps, 1963) and another in the U.S.A. (Bock, 1960a).

The history of the Huia's disappearance, and many aspects of its life and habits, are summarized by Phillipps. Last reported alive in 1907, it is probable that some survived after this date, and Phillipps entertains the possibility that a few may still exist. Its range was restricted to the mountainous Wellington Province of North Island, New Zealand. Here, the combination of a mild climate and heavy rainfall has produced densely forested country with a high incidence of timber decay and epiphytic growth. The Huia fed principally on insects, varied with some vegetable matter, but by far the most important prey appears to have been the larvae of the Huhu beetle, *Prionoplus reticularis* (Cerambycidae). This large beetle is common in many parts of New Zealand, and its larvae, found in decaying timber, may reach a length of 70 mm and a width of 20 mm. The most detailed account of the Huia's manner of extracting these is provided by Buller (1888). This account has been often quoted, but because of its relevance to the present study, it seems essential to do so again. Buller's description refers to a pair of captive Huias which at first he fed on individual huhu grubs:

'On offering one of these to the Huia he would seize it in the middle, and, at once transferring it to his perch and placing one foot firmly upon it, he would tear off the hard parts, and then throwing the grub upwards to secure it lengthwise in his bill, would swallow it whole . . . They seemed never to tire of probing and chiselling with their beaks. Having discovered that the canvas lining of the room was pervious, they were incessantly piercing it, and tearing off large strips of paper, till, in the course of a few days, the walls were completely defaced.

But what interested me most of all was the manner in which the birds assisted each other in their search for food, because it appeared to explain the use, in the economy of nature, of the differently formed bills in the two sexes. To divert the birds, I introduced a log of decayed wood infested with the huhu grub. They at once attacked it, carefully probing the softer parts with their bills, and then vigorously assailing them, scooping out the decayed wood till the larva or pupa was visible, when it was carefully drawn from its cell, treated in the way described above, and then swallowed. The very different development of the mandibles in the two sexes enabled them to perform separate offices. The male always attacked the more decayed portions of the wood, chiselling out his prey after the manner of some Woodpeckers, while the female probed with her long pliant bill the other cells, where hardness of the surrounding parts resisted the

chisel of her mate. Sometimes I observed the male remove the decayed portion without being able to reach the grub, when the female would at once come to his aid, and accomplish with her long slender bill what he had failed to do. I noticed, however, that the female always appropriated to her own use the morsels thus obtained.'

An additional reference to the different feeding techniques of male and female is the note by J. M. Wright quoted by Oliver (1955):

'I have watched them in pairs hunting for wetas.\* The male would tear away at the outer part of a green sapling. The female then tried to retrieve the weta with her long slender bill. If not successful she would stand back while the male tried to enlarge the hole. Unless the tree was a maire the birds would generally succeed and would then fly away with the weta.'

Phillipps (1963) also provides the most detailed information available on the extent of dimorphism ascertainable from skins, and on the range of variation in the two sexes, based on 119 specimens in New Zealand museums. Young birds show little difference in size and shape of the bill. Some male bills were more curved than usual, but were normally deeper than those of females. The male bills reached an extreme length of 59–60 mm (from feathers), and females up to 104 mm. Phillipps mentions two doubtful cases of birds with bills 63 mm long which he has treated as males, though they may be females. The skin collection of the British Museum (Natural History) includes two doubtful individuals; one, with a bill length of 76.4 mm is labelled as a male; the other, labelled as a female, has a bill of 71.8 mm. Excluding these, bill length data for other specimens in the collection may be summarized as follows:

Males: Mean 59.7; Min. 54.7; Max. 65.0 (16 specimens).  
 Females: Mean 96.3; Min. 87.1; Max. 108.0 (7 specimens).

Buller (1878) also gives details on the range of bill form in the Huia and figures several specimens, including a female with the upper jaw much longer than the lower, recalling some species of *Hemignathus* (Drepanididae).

## II. METHODS AND MATERIAL

Most of the observations reported here were obtained simply by dissection using a stereomicroscope at powers mainly in the range  $\times 2\frac{1}{2}$  to  $\times 20$ . The main complicating factor was the irreplaceable nature of the Huia specimens, and because of this, it was thought prudent to keep dissections of this species to a minimum. In general, dissections have been limited to the left side, and as little structure as possible has been removed. Because of its history, the single specimen of *Creadion carunculatus* was regarded as of similar value, and no dissections were attempted which would have required removing or severing structures.

For convenient reference, the Huia specimens were given a simple individual coding in addition to their British Museum (Natural History) Registration numbers.

\* Orthoptera, Gryllacridoidea.

Details of the specimens of Callaeidae used, with their conditions at commencement of the study, are as follows :

*Heteralocha acutirostris*

- ♂ 1. Reg. No. A 1973.1.3. Intact spirit specimen.  
 ♂ 2. Reg. No. A 1973.1.2. Intact spirit specimen.  
 ♂ 3. Reg. No. 1940.12.8.107. Intact spirit specimen.  
 ♂ 4. Reg. No. 81.1.17.91. Complete skeleton specimen.  
 ♀ A. Reg. No. A 1973.1.4. Spirit specimen with skull almost completely skeletonized. Rhamphotheca of upper jaw retained (but detached), tongue, hyoid muscles, M. depressor mandibulae and all neck muscles intact.  
 ♀ B. Reg. No. A 1973.1.1. Spirit specimen with cranium and upper jaw completely skeletonized, removed and maintained as dried specimen. Upper jaw broken and rhamphotheca missing. Lower jaw with rhamphotheca intact, detached, but retained in spirit. Tongue, hyoid muscles and all neck muscles intact.  
 ♀ C. Reg. No. 1940.12.8.108. Intact spirit specimen.

*Creedion carunculatus*

Reg. No. 1845.2.21.392. Spirit specimen with skull detached and skeletonized except for M. depressor mandibulae which is intact. Rhamphotheca of both jaws missing. Tongue, hyoid muscles and all neck muscles intact. This specimen is believed to have been collected on Captain Cook's third voyage (Burton, 1969). It is probably the oldest surviving spirit specimen of any bird, but is in good condition.

*Callaeas cinerea*

Reg. Nos. A 1973.1.5 and A 1973.1.6. 2 intact spirit specimens.

Various spirit, skeleton or skin specimens of birds in other families were also examined for comparative purposes. The species involved are mentioned in the text or in the tables.

### III. SKULL AND LIGAMENTS

The skull of a male Huia was described and figured by Garrod (1872), who called attention to some of its conspicuous features. A short description of the skull is also given by Oliver as an appendix to the book by Phillipps (1963). The skulls of male and female specimens are depicted in Figs. 1-3. It will be noted that with the rhamphotheca removed, the disparity between the sexes in jaw form appears much less than in skin specimens; this is due to the much greater development of the rhamphotheca in the female. Striking features of the skull in both sexes (though more marked in the male) are the prominent occipital crest, well-developed exoccipital process and very long retroarticular process. Less obvious, but equally

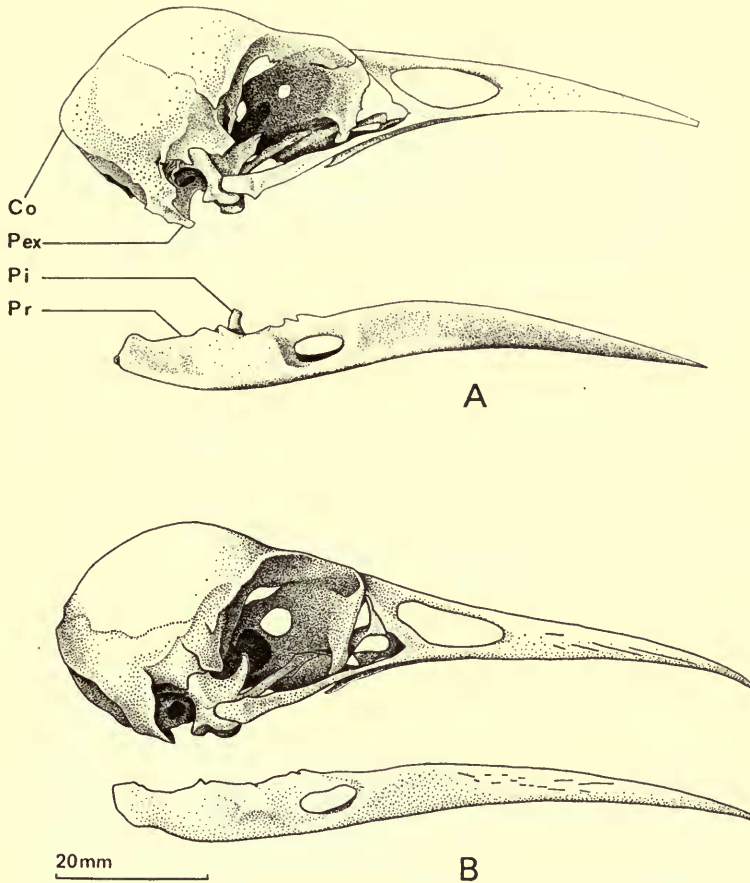


FIG. 1. *Heteralocha acutirostris*, skull in lateral view. A. Male ( $\sigma$  4). B. Female ( $\text{♀}$  A).  
For abbreviations see p. 47.

unusual, is the position and form of the nasal-frontal hinge. The nasals extend backward in the form of a rounded spur, reaching a point roughly level with the middle of the orbits. The nasal-frontal hinge is consequently situated much further posteriorly than in typical passerines; the drawings of *Creadion* and *Callaeas* (Figs. 4-9) show the normal condition.

Quantitative data for the specimens studied are summarized in Table 1. Relative values for the various measurements taken have been assigned by giving for each its ratio to length of the jugal bar. Several other ratios are also included. In the absence of weight data, sternum length is used as a crude index of body size (Amadon, 1943; Zusi, 1962); measurements of wing, tail and tarsus are also given (*R* to *U*).

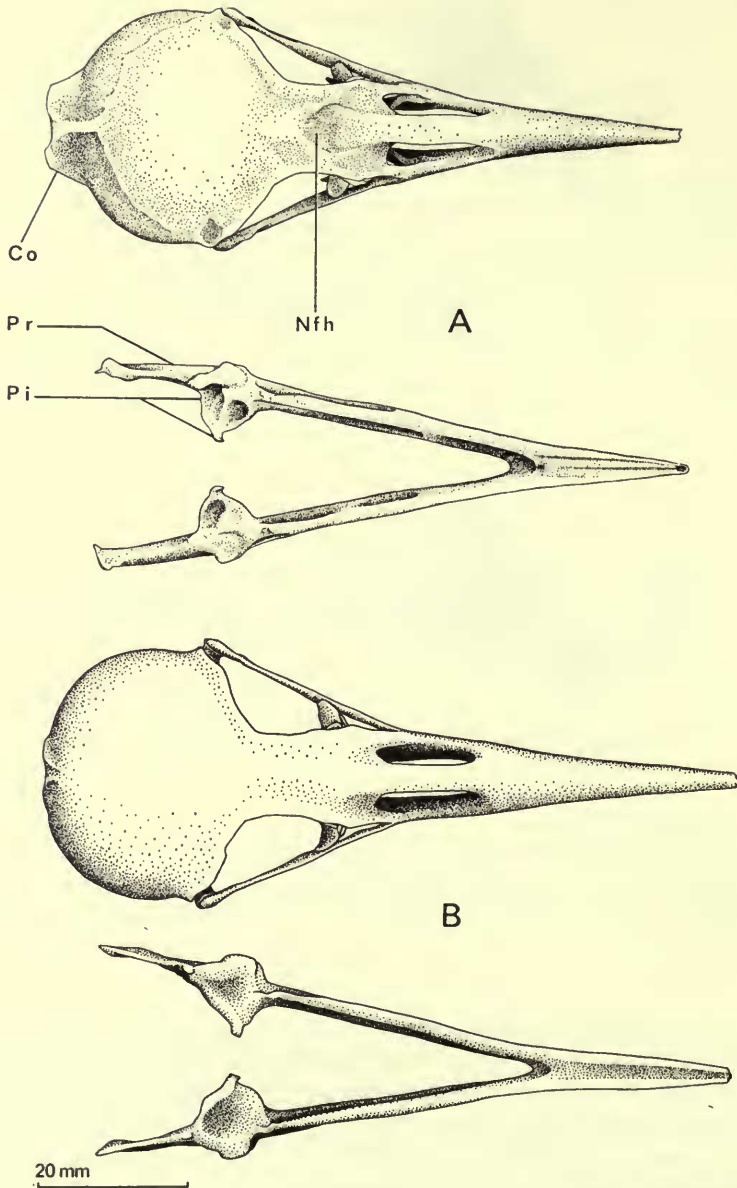


FIG. 2. *Heteralocha acutirostris*, skull in dorsal view.  
 A. Male (♂ 4). B. Female (♀ A). For abbreviations see p. 47.



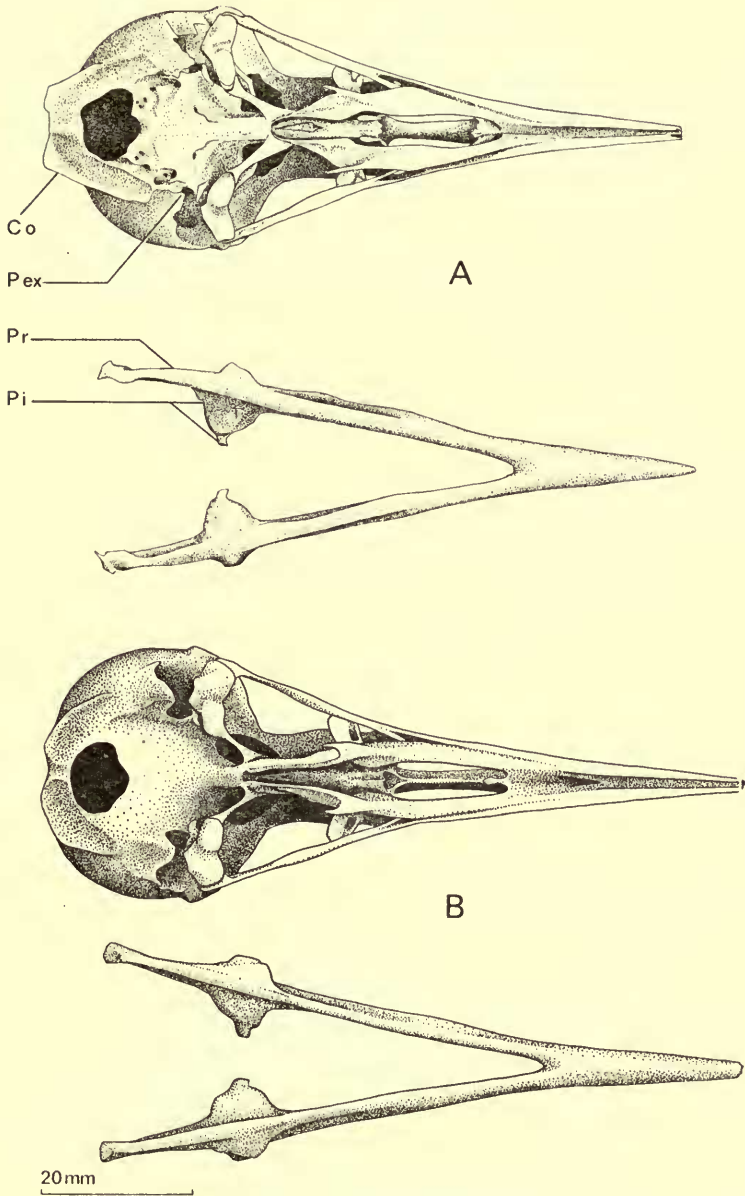


FIG. 3. *Heteralocha acutirostris*, skull in ventral view.  
 A. Male (♂ 4). B. Female (♀ A). For abbreviations see p. 47.

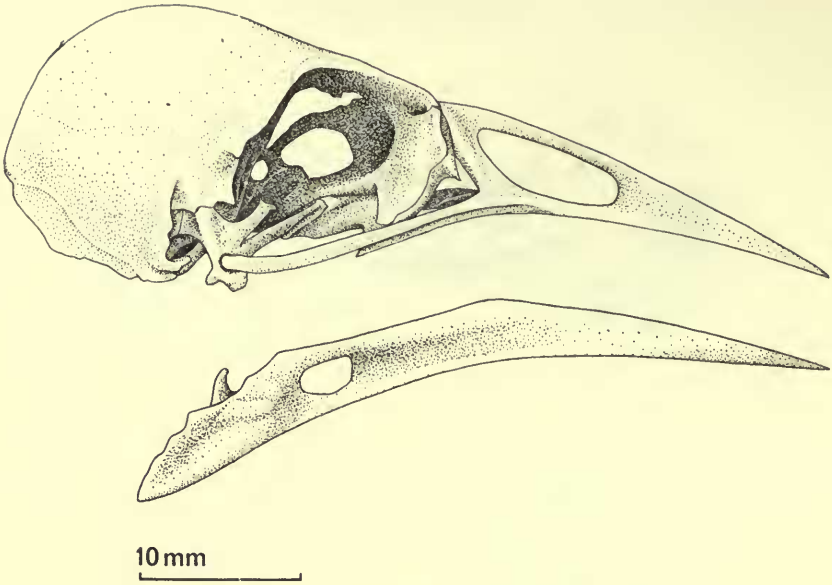


FIG. 4. *Creadion carunculatus*, skull in lateral view.

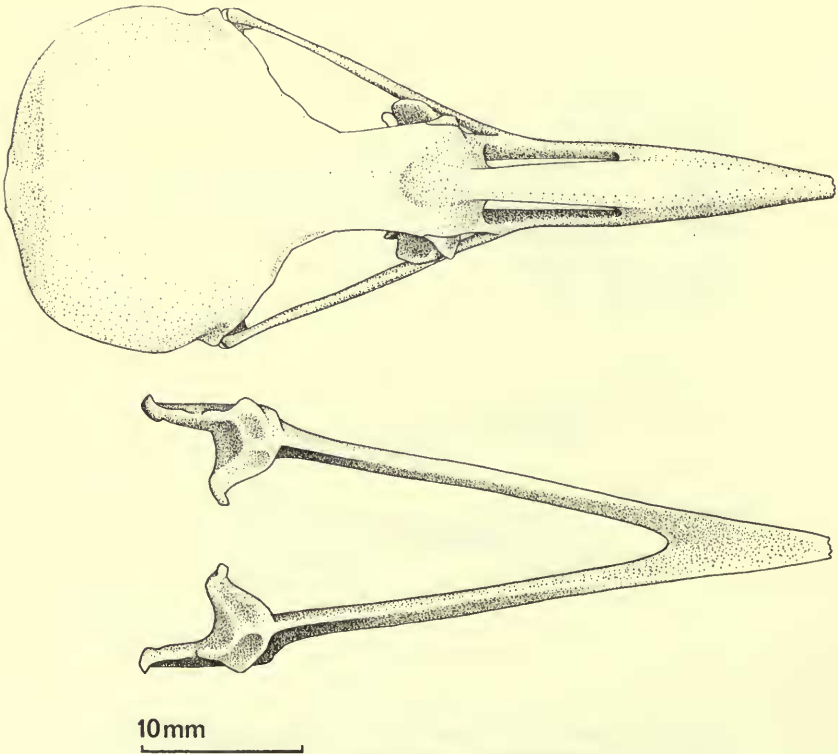


FIG. 5. *Creadion carunculatus*, skull in dorsal view.

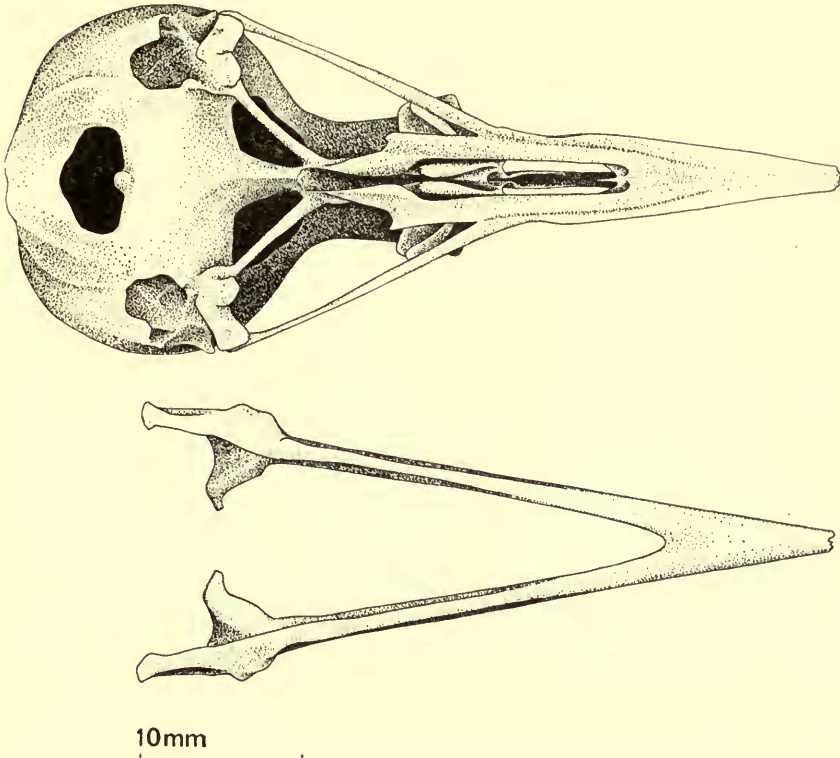


FIG. 6. *Creadion carunculatus*, skull in ventral view.

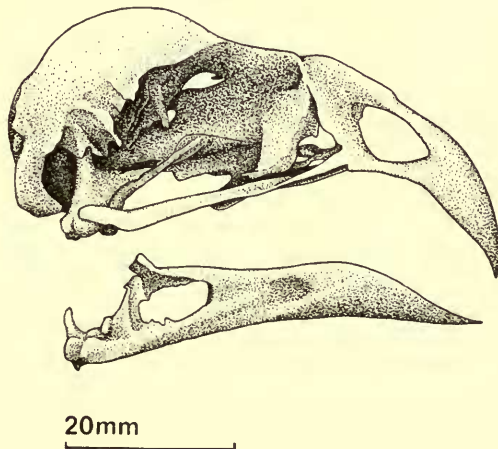
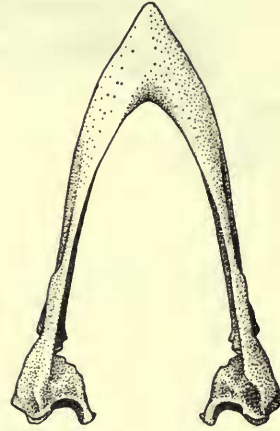
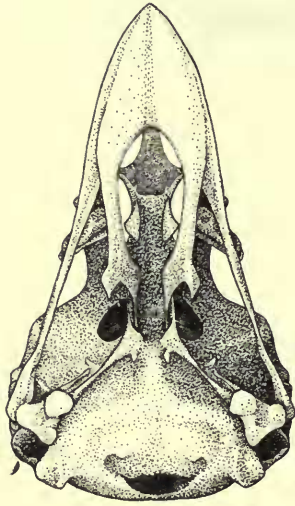
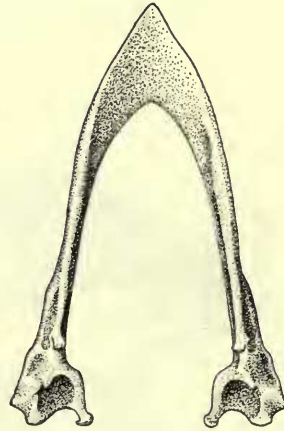
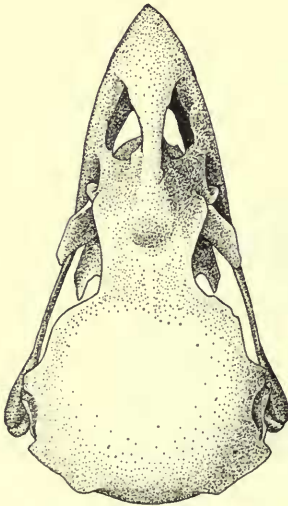


FIG. 7. *Callaeas cinerea*, skull in lateral view.



20mm

FIG. 9. *Callaeas cinerea*, skull in ventral view.

20mm

FIG. 8. *Callaeas cinerea*, skull in dorsal view.

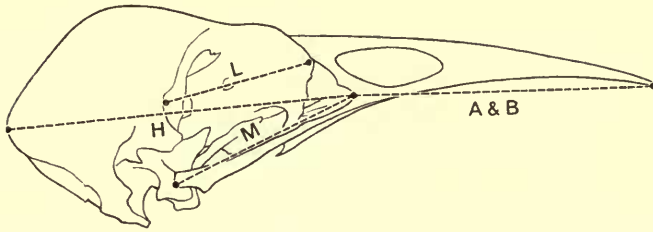


FIG. 10. Skull of *Heteralocha acutirostris* showing the method of taking various measurements given in Table 1. For key see below.

The methods by which skeleton measurements were taken are as follows :

- A Upper jaw length : Fig. 10.
- B Upper jaw with rhamphotheca removed : Fig. 10.
- C, D Lower jaw : tip of mandible to posterior tip of retroarticular process, with and without rhamphotheca.
- E Retroarticular process : measured from the posterior edge of the lateral condyle of the quadrate.
- F Bill depth : measured at right angles to the tomia, level with the junction of nasal and jugal bars. Only given for specimens with rhamphotheca intact on both jaws.
- G Bill width : measured at the same point as F, with or without rhamphotheca.
- H Cranium length : Fig. 10.
- J Cranium breadth : the greatest breadth of the cranium (just posterior to the orbits).
- K Anterior cranium breadth : the maximum breadth of the cranium anterior to the orbits.
- L Orbit length : Fig. 10.
- M Jugal bar : Fig. 10.
- N Quadrate : from the lateral extremity of the articulation with the jugal bar, to the medial tip of the orbital process.
- O Pterygoid : from the anterior to the posterior extremities visible in antero-lateral view.
- P Tongue length : from the anterior tip to the tips of the postero-lateral papillae.
- Q Sternum length : from the midpoint of the posterior margin to the antero-ventral tip of the keel.

The postorbital, internal jugo-mandibular and occipito-mandibular ligaments are present. Strong connective tissue running from the postorbital process to the ectethmoid process across the ventral lateral side of the orbit amounts to an ill-defined suborbital ligament. There is no external jugo-mandibular ligament. The occipito-mandibular ligament is extremely stout, and much of its central region is ossified, more so in male specimens. The internal jugo-mandibular ligament contains two

TABLE I  
Quantitative data for the specimens of Callaeidae used in this study

	<i>Heteralocha</i> ♂ 1	<i>Heteralocha</i> ♂ 2	<i>Heteralocha</i> ♂ 3	<i>Heteralocha</i> ♂ 4	<i>Heteralocha</i> ♀ A	<i>Heteralocha</i> ♀ B	<i>Heteralocha</i> ♀ C	Mean of ♂ specimens	Mean of ♀ specimens	<i>Creadion</i> 1845.2.21.392	<i>Callaas</i> 1940.12.8.109	<i>Callaas</i> (Bennett Esq.)
A	Upper jaw length	50.4 (1.83)	50.0 (1.80)	50.3 (1.82)	—	98.9 (3.73)	82.1 (3.17)	50.2 (1.82)	90.0 (3.45)	—	25.1 (0.78)	—
B	Upper jaw, rhamphotheca removed	44.8 (1.63)	44.7 (1.61)	46.0 (1.66)	38.6 (1.42)	48.4 (1.82)	—	43.5 (1.58)	49.7 (1.89)	23.0 (1.33)	24.5 (0.76)	20.2 (0.66)
$\frac{A-B}{A}$	Index of relative rhamphotheca development	0.11	0.11	0.09	—	0.51	0.38	0.10	0.45	—	0.02	—
C	Lower jaw length	91.9 (3.34)	88.3 (3.18)	87.9 (3.17)	—	—	108.9 (4.24)	89.4 (3.23)	109.5 (4.25)	—	51.0 (1.59)	—
D	Lower jaw, rhamphotheca removed	86.8 (3.16)	84.1 (3.03)	85.3 (3.08)	78.3 (2.88)	80.1 (3.02)	84.8 (3.30)	83.6 (3.04)	84.2 (3.24)	44.1 (2.55)	50.3 (1.57)	45.9 (1.49)
E	Retroarticular process	15.1 (0.55)	16.5 (0.59)	17.6 (0.63)	15.2 (0.56)	14.0 (0.53)	13.5 (0.53)	16.1 (0.58)	13.7 (0.53)	8.0 (0.46)	nil	nil
E/C	Retroarticular process relative to total lower jaw	0.16	0.19	0.20	—	—	0.12	0.18	0.12	—	—	—

<i>F</i>	Bill depth	20.5 (0.75)	19.7 (0.71)	19.5 (0.70)	-	-	16.5 (0.64)	19.9 (0.72)	16.5 (0.64)	9.8 (0.57)	19.6 (0.61)	17.8
<i>G</i>	Bill width	12.0 (0.44)	12.5 (0.45)	11.9 (0.43)	12.2 (0.45)	10.0 (0.38)	10.2 (0.40)	12.1 (0.44)	10.3 (0.40)	5.9 (0.34)	15.3 (0.48)	13.8 (0.58)
<i>H</i>	Cranium length	45.6 (1.66)	47.4 (1.70)	47.4 (1.71)	45.1 (1.66)	42.8 (1.61)	42.8 (1.67)	46.4 (1.68)	42.9 (1.65)	29.4 (1.70)	39.4 (1.23)	39.2 (1.27)
<i>J</i>	Cranium breadth	30.0 (1.09)	32.8 (1.18)	31.8 (1.15)	29.9 (1.10)	28.2 (1.06)	28.0 (1.09)	31.1 (1.13)	28.3 (1.09)	20.5 (1.18)	28.7 (0.89)	29.3 (0.95)
<i>K</i>	Anterior cranium breadth	14.8 (0.54)	13.7 (0.49)	13.4 (0.48)	13.9 (0.51)	12.0 (0.45)	11.7 (0.44)	13.9 (0.50)	11.9 (0.45)	8.4 (0.49)	15.6 (0.49)	14.8 (0.48)
<i>L</i>	Orbit length	19.2 (0.70)	18.4 (0.66)	19.0 (0.69)	18.5 (0.68)	18.4 (0.69)	17.7 (0.69)	18.8 (0.68)	18.0 (0.69)	12.5 (0.72)	20.2 (0.63)	21.0 (0.68)
<i>M</i>	Jugal bar length	27.5 (1.00)	27.8 (1.00)	27.7 (1.00)	27.2 (1.00)	26.5 (1.00)	25.7 (1.00)	27.5 (1.00)	26.0 (1.00)	17.3 (1.00)	32.1 (1.00)	30.8 (1.00)
<i>N</i>	Quadrate	13.3 (0.48)	13.4 (0.48)	-	1.36 (0.50)	12.5 (0.47)	12.4 (0.48)	13.4 (0.49)	12.3 (0.47)	7.3 (0.42)	12.7 (0.40)	-
<i>O</i>	Pterygoid length	-	-	-	13.6 (0.50)	14.1 (0.53)	13.2 (0.51)	13.6 (0.50)	13.6 (0.52)	7.4 (0.43)	16.5 (0.51)	-
<i>P</i>	Tongue length	31.5 (1.15)	29.9 (1.08)	31.7 (1.14)	-	30.1 (1.14)	31.8 (1.24)	32.1 (1.24)	31.3 (1.21)	-	21.4 (0.67)	18.2 (0.59)
<i>Q</i>	Sternum length	40.5	40.4	38.9	37.3	37.0	36.0	35.8	36.3	18.3	35.2	-
<i>M/Q</i>	Skull to body index	0.68	0.69	0.71	0.73	0.72	0.71	0.72	0.70	0.95	0.91	-
<i>R</i>	Culmen from feathers	59.8	57.2	57.2	-	108.0	-	99.6	58.1	103.8	-	-
<i>S</i>	Wing (maximum chord)	202	195	197	-	192	197	200	198	92	157	147
<i>T</i>	Tail	200	182	-	-	192	193	204	91	196	154	-
<i>U</i>	Tarsus	86.3	83.1	80.5	82.4	76.5	78.8	75.8	83.1	77.0	68.7	67.6

Each head measurement is followed (in brackets) by its ratio to jugal length. Blank spaces indicate that measurements could not be made owing to missing structures or the presence of intervening tissue.

sesamoids, one placed laterally and the other posterior to the quadrate. In common with all passerines so far studied, the lower jaw has no medial brace (see Bock, 1960b).

#### IV. JAW MUSCULATURE

A work of major importance for studies of avian jaw musculature is Lakjer's (1926) review of the trigeminal musculature. For passerines in particular, the paper by Fiedler (1951) provides valuable clarification. Investigations by Bock (1960a and MS) have resolved many remaining problems of structure and terminology within the order, and his nomenclature for the subdivision of complex muscles is the one followed here. The jaw musculature of the Callaeidae remains undescribed beyond the comments of Garrod (1872) and Lowe (1938) on the large size of the 'digastric muscle' (= *M. depressor mandibulae*).

In describing the structure of complex muscles it is often useful to designate their various aponeuroses by letters or numbers. It is far from clear to what extent these aponeuroses can be homologized between different groups, although the work of Starck and Barnikol (1954) has made progress in this respect for *M. adductor mandibulae externus*. In the present case, a simple numbering system has been used where necessary, but is not intended to imply homology with any numbered aponeuroses described from other species, with the exception of Aps. 1, 2 and 3 in *M. adductor mandibulae externus*.

##### *M. adductor mandibulae externus*

This important and complex muscle acts to raise the lower jaw and to maintain a grip on objects held in the bill. Its architecture is intricate, and the relationships of its aponeuroses can be better understood by the examination of cross sections (Fig. 18). The abbreviation 'M.a.m.e.' is used in parts of the description to shorten the otherwise unwieldy names of some subdivisions. The three major aponeuroses described by Starck and Barnikol (1954) in a wide range of birds of several orders can be recognized with little difficulty in *Heteralocha*, and their numbering here (Aps. 1, 2 and 3) is the same as Starck and Barnikol's.

##### *M. adductor mandibulae externus rostralis*

The most dorsal part of *M. adductor mandibulae externus*, with an extensive fleshy origin on the cranium. Insertion is made principally via Ap. 1, which narrows anteriorly to form a flat tendon attached to a crista on the surangular. Following Bock, three sections are recognized :

*M.a.m.e. rostralis medialis.* Origin is from the postero-lateral border of the orbit, medial to the postorbital process, and from a vertically oriented aponeurosis (Ap. 4) attached to the orbit along the medial border of the muscle. Insertion is made via Ap. 1. Medially, a group of fibres from the ventral part of the muscle overlaps part of Ap. 1 as a more or less distinct slip.

*M.a.m.e. rostralis temporalis.* Origin is fleshy from the border of the temporal fossa ; a short aponeurosis (Ap. 5) runs forwards from the tip of the postorbital



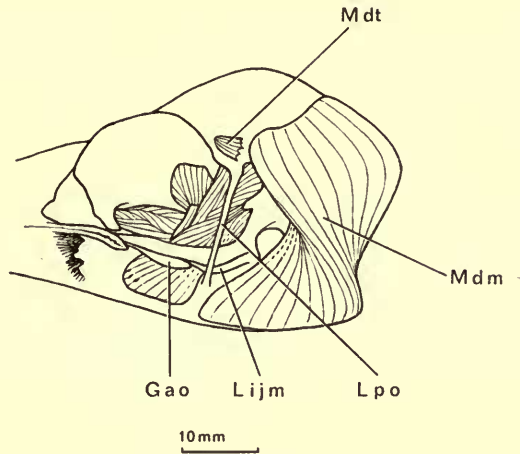


FIG. 11. *Heteralocha acutirostris*, male ( $\sigma$  1), jaw muscles and ligaments.  
For abbreviations see p. 47.

process across the dorsal lateral surface, and in some specimens extends onto the dorsal surface of M.a.m.e. rostralis medialis. The fibres of this section converge anteriorly, falling into an ill-defined bipinnate arrangement, and are attached to the ventro-lateral surface of Ap. 1; a few fibres overlap its dorsal surface posteriorly, but it is exposed for some 8 mm from the insertion.

M.a.m.e. rostralis lateralis. This section lies superficial to the dorsal part of M.a.m.e. ventralis. Its origin is from the lateral edge of the zygomatic process, and from the lateral edge of Ap. 2 in its narrow posterior region. Fibres run upward and medially from the origin and insert on the lateral surface of the mandible over a narrow zone dorsal to the insertion of M.a.m.e. ventralis. This insertion is fleshy, and via a superficial aponeurosis (Ap. 6) which merges medially with Ap. 1. The anterior ventral part of this section lies medial to the jugal bar and is in consequence flattened into a relatively thin sheet of fibres.

*M. adductor mandibulae externus ventralis*

Origin is from the zygomatic process, by a strong aponeurosis (Ap. 2) which traverses the gap between the cranium and mandible as a fairly narrow tendon, then fans out over the lateral surface of the muscle. Fibres arising from this aponeurosis make an extensive fleshy insertion on the lateral surface of the mandible, spanning the fenestra in the posterior part of the mandible.

*M. adductor mandibulae externus caudalis*

The shortest section of *M. adductor mandibulae externus*. Origin is from the otic process of the quadrate and from the ventral surface of the posterior half of Ap. 2. The origin is fleshy, and by a weak aponeurosis (Ap. 7). Insertion is on the dorsal lateral edge of the surangular, posterior and ventral to that of Ap. 1. The insertion is made by a short, narrow aponeurosis (Ap. 3), which bifurcates within

the body of the muscle to form a dorsal (Ap. 3a) and a ventral (Ap. 3b) branch. Ap. 7 passes between 3a and 3b before fading out. The muscle shows multipinnate structure, clearest in its middle third, and most conspicuous about Ap. 3a. Fibres run forwards from Ap. 2 to Ap. 3a, back from Ap. 3a to Ap. 7, and forwards again from Ap. 7 to Ap. 3b.

*M. pseudotemporalis superficialis*

A muscle of relatively simple structure, whose action is adduction of the lower jaw. The origin is a broad fleshy one on the posterior wall of the orbit, immediately medial to M.a.m.e. rostralis medialis. There is also a weak dorsal aponeurosis attached to the orbit. Insertion is made via a strong tendon attached to the medial side of the surangular, ventral to the ramus mandibularis of the trigeminal nerve.

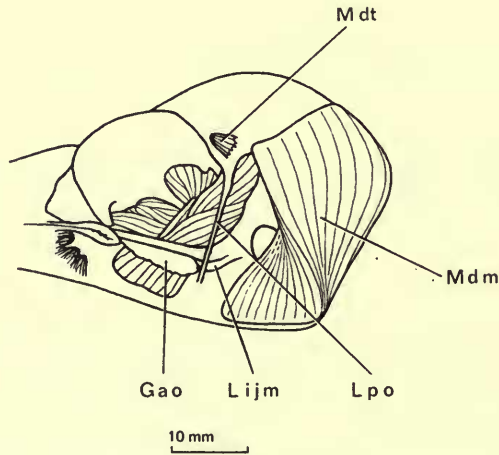


FIG. 12. *Heteralocha acutirostris*, female (♀ C), jaw muscles and ligaments.  
For abbreviations see p. 47.

*M. pseudotemporalis profundus*

This muscle is an adductor of the lower jaw, and by its action on the quadrate it also functions to lower the upper jaw. It takes its origin from the dorso-lateral surface of the orbital process of the quadrate, and from a strong aponeurosis attached to the expanded tip of the orbital process. It makes an extensive fleshy insertion on the medial surface of the mandible, overlapping slightly onto its dorsal edge, adjacent to Ap. 1 of M.a.m.e. rostralis.

*M. adductor mandibulae posterior*

The actions of this muscle are similar to those of *M. pseudotemporalis profundus*. Due to its situation closer to the mandible-quadrate articulation, it has a lower mechanical advantage, but its upward component may be of value in holding the mandible against the quadrate. *M. adductor posterior* is contiguous with *M.*

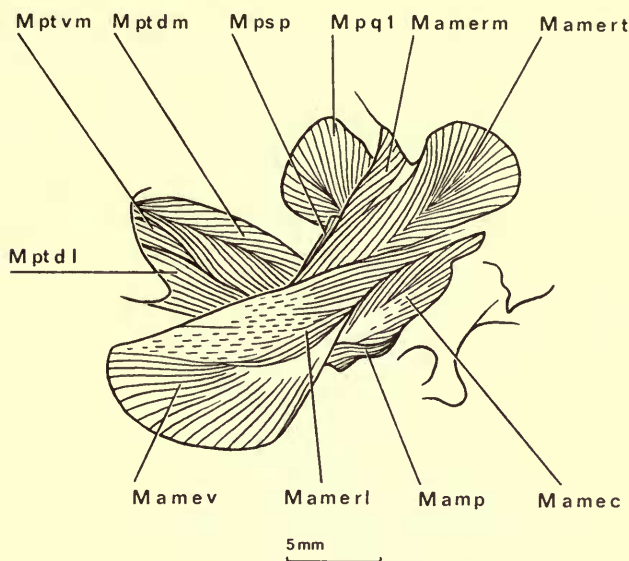


FIG. 13. *Heteralocha acutirostris* (♂ 1), jaw muscles in lateral view.  
For abbreviations see p. 47.

pseudotemporalis profundus at its origin, which is also a fleshy one on the quadrate, occupying the base of the orbital process and the dorsal surface of the quadrate body. The two muscles are separated (following the criterion used by Lakjer, 1926) by *N. pterygoideus*. The muscle inserts on the expanded region of the dorsal surface of the mandible just anterior to the base of the internal process, and posterior to the insertion of *M.a.m.e. caudalis*. The insertion is fleshy and via a weak dorsal aponeurosis.

#### *M. pterygoideus*

This important muscle complex acts both to lower the upper jaw and to raise the lower. Its attachments to the palatine and pterygoid are arbitrarily regarded as the origin, and attachment to the lower jaw as the insertion.

#### *M. pterygoideus dorsalis lateralis*

This section has an extensive fleshy origin on the dorsal surface of the palatine. It inserts on the medial surface of the mandible, posterior to *M. pseudotemporalis profundus*, fleshily, and by a superficial aponeurosis (*Ap. 1*), which is strongest ventrally.

#### *M. pterygoideus ventralis lateralis*

Origin is from an aponeurosis (*Ap. 2*) which is attached to the postero-lateral tip of the palatine, and extends for some distance across the ventral surface of the muscle. The medial edge of this aponeurosis serves to demarcate it from *M. pterygoideus*

ventralis medialis seen in ventral view. *M. pterygoideus ventralis lateralis* is attached at the base of the internal process of the mandible, ventral to the insertion of *M. pterygoideus dorsalis lateralis*. There is no overlap ('venter externus') onto the ventral edge or lateral surface of the mandible as in many birds, since the ventral medial edge of the mandible in this region is occupied by a forward extension of *M. depressor mandibulae*.

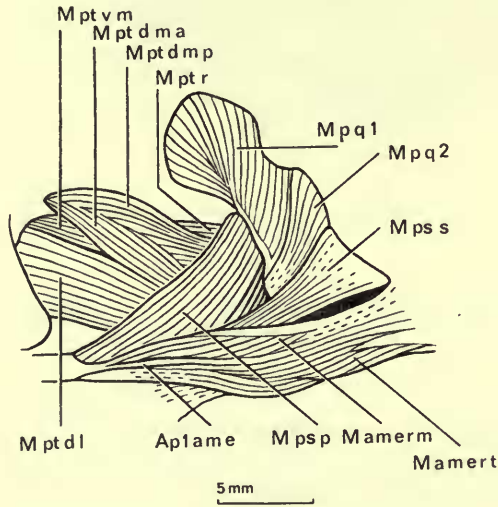


FIG. 14. *Heteralocha acutirostris* (♂ 1), jaw muscles in dorsal view.  
For abbreviations see p. 47.

#### *M. pterygoideus dorsalis medialis*

In dorsal view, this muscle is seen to lie immediately adjacent and posterior to *M. pterygoideus dorsalis lateralis*, separated from it by a narrow groove which widens medially, exposing a small area of the dorsal surface of *M. pterygoideus ventralis medialis*. Its origin is confined to the pterygoid, and occupies much of its surface. The muscle falls into anterior and posterior portions, whose fibres diverge in a posterior direction roughly along the lines of the pterygoid, so that it appears bipinnate in dorsal view.

*M. pterygoideus dorsalis medialis* anterior originates more laterally on the pterygoid, and inserts narrowly on the mandible, immediately caudal to *M. pterygoideus dorsalis lateralis*. The insertion is fleshy and aponeurotic, the aponeurosis (Ap. 3) being strongest ventrally.

*M. pterygoideus dorsalis medialis* posterior originates medially on the pterygoid, and fans out to a wide fleshy insertion on the dorsal part of the internal process of the mandible, dorsal to that of *M. pterygoideus ventralis medialis*.

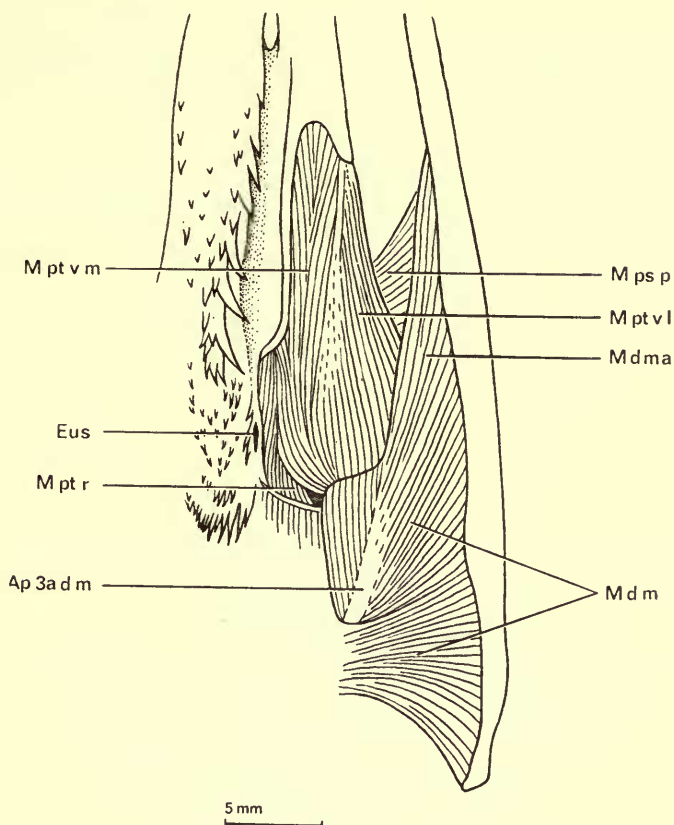


FIG. 15. *Heteralocha acutirostris* (♂ 1). *M. pterygoideus* and *M. depressor* in ventral view. Left side of palate left intact to show papillae. For abbreviations see p. 47.

*M. pterygoideus ventralis medialis*

There is an extensive fleshy origin on the ventral surface of the palatine and insertion is made on the internal process of the mandible, fleshily, and by a strong dorsal aponeurosis (Ap. 4). The fibres of this section are orientated more nearly parallel to the skull axis than those of any other part of *M. pterygoideus*. On the medial side of the muscle is a slip (*M. pterygoideus retractor*) exclusively specialized for retracting the palatal apparatus, attached at one end to the medial caudal tip of the palatine, and at the other to the basitemporal plate of the skull. A few of its most medial fibres are attached to the edges of the opening of the Eustachian tube.

*M. protractor quadrati et pterygoidei*

This muscle acts to raise the upper jaw by moving the palatal framework and jugals forwards. It has a wide fleshy origin from the posterior part of the interorbital septum and the adjacent region of the posterior orbital wall. The lateral border of the muscle lies immediately adjacent to *M. pseudotemporalis superficialis*.

Two parts can be distinguished. The more anterior and medial part (*M. protractor 1*), arising mainly on the interorbital septum, shows a bipinnate fibre arrangement. Its raphe is a strong aponeurosis attached to a spur on the posterior dorsal tip of the pterygoid, immediately adjacent to the quadrate. This raphe serves as the principal site of insertion for the fibres of *M. protractor 1*.

The lateral part (*M. protractor 2*) originating from the posterior wall of the orbit inserts fleshily, and by a weak dorsal aponeurosis on the caudal edge of the basal half of the orbital process.

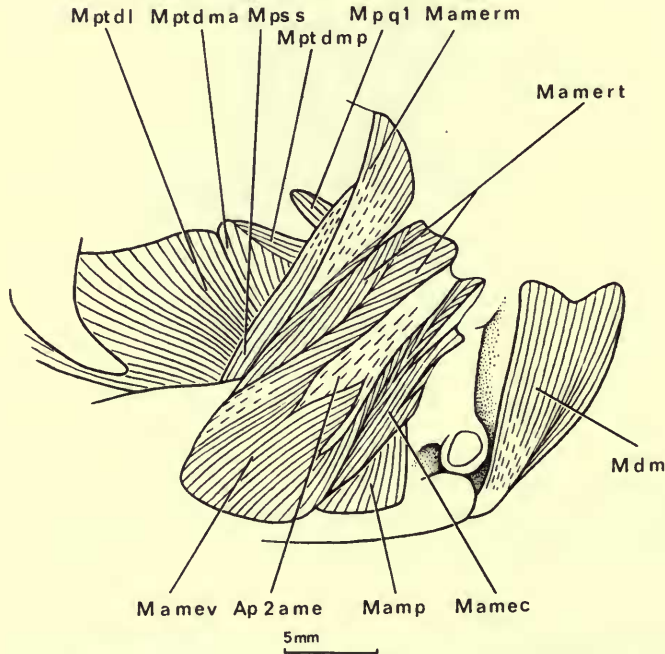


FIG. 16. *Callaeas cinerea*, jaw muscles in lateral view. For abbreviations see p. 47.

### *M. depressor mandibulae*

This muscle, which depresses the lower jaw, is of enormous bulk (and, presumably, fibre number) in *Heteralocha* relative to the other jaw muscles. There is a wide fleshy origin on the squamosal, parietal and exoccipital. Fibres originating high on the cranium converge to insert fleshily near the extremity of the long retroarticular process, mainly on its medial side. Those originating lower, on the exoccipital, fan out to insert fleshily on both surfaces of the retroarticular process. Fibres inserting medially extend far forward beyond the retroarticular process along the ventral half of the mandible, ventral to the insertion of *M. pseudotemporalis profundus*. This extension is here termed the pars anterior of *M. depressor mandibulae*.

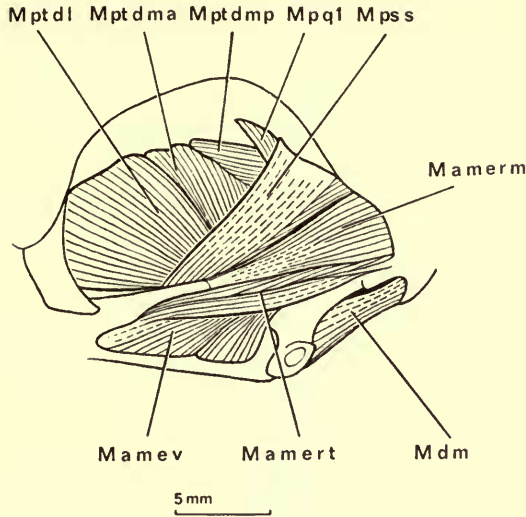


FIG. 17. *Callaeas cinerea*, jaw muscles in dorsal view. For abbreviations see p. 47. M. pseudotemporalis profundus is concealed by M. pseudotemporalis superficialis.

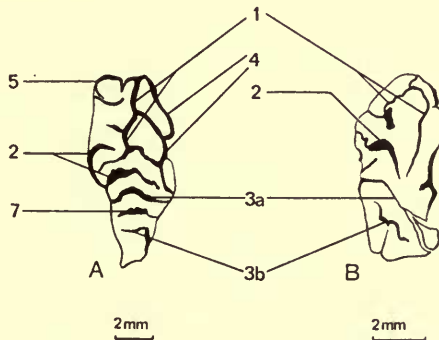


FIG. 18. M. adductor mandibulae externus, TS at about the midpoint of the otic process of the quadrate, and at right angles to it. Numbering of aponeuroses as explained in text. A - *Callaeas cinerea*. B - *Heteralocha acutirostris* (♂ 1). The left side is lateral in both diagrams.

The following aponeuroses can be distinguished :

- Ap. 1. This is attached to the cranium around the dorsal edge of the origin on the squamosal and parietal, and extends some way across the lateral surface of the muscle.
- Ap. 2. A strong aponeurosis with a narrow attachment at about the middle of the posterior border of the auditory meatus, fanning out across the lateral surface of the muscle, and acting as a surface of origin for fibres inserting on the anterior half of the lateral surface of the retroarticular process.

- Ap. 3. A strong aponeurosis attached to the occipital crest, which marks the postero-ventral limit of the origin. Ap. 3 extends some way across the medial surface of the muscle, and becomes stronger on the exoccipital process, whence it is produced as a strong raphe (Ap. 3a) across the ventral region of the muscle, and on into the pars anterior. Fibres arising from its medial side insert mainly on the medial surface of the internal process of the mandible. Those running from its lateral side insert on the medial surface of the basal half of the long retroarticular process, on the posterior face of the internal process at its base, and on the ventral medial surface of the mandible.
- Ap. 4. An aponeurosis attached to the dorsal edge of the internal process of the mandible, extending across much of the dorsal surface of the short part of the muscle between this and the exoccipital. This aponeurosis is branched and infolded within the muscle.
- Ap. 5. An aponeurosis attached to the dorsal edge of the retroarticular process, but concealed from lateral view by the thin sheet of fibres originating from Ap. 2, and inserted on the lateral surface of the process.

#### V. BUCCAL CAVITY AND GLANDS

Backwardly directed horny papillae are abundant on the surface of the palate. They are longest where they fringe the choanae, and in a densely clustered transverse row posterior to the internal opening of the Eustachian tubes. The surface of the larynx is also papillate, the papillae being longest at its posterior margin.

Three pairs of salivary glands are present. The *Gl. angularis oris* lies on the side of the head immediately below the skin and just ventral to the jugal bar; its duct opens at the angle of the gape. A second gland, which may be termed a *Gl. palatinae* (see Antony, 1920), lies between *M. depressor mandibulae*, pars anterior, and *M. pterygoideus ventralis lateralis*, immediately below the mucosa of the palate. The third gland is a sublingual one. It lies immediately lateral to *M. genioglossus*, and extends from the level of the anterior border of *M. mylohyoideus* to the region of the tongue base. Its duct runs alongside *M. genioglossus*, but diverges from it near the mandibular symphysis to open in a lateral position.

#### VI. TONGUE APPARATUS

The tongue is narrow, tapering evenly towards its anterior tip which is somewhat frayed and brush like (Fig. 19). The lateral edge bears a few papillae posteriorly, and the posterior edge is crowded with pointed papillae, longest laterally. Tongue length for the specimens examined is shown in Table I.

The tongue skeleton is similar to that of many passerines. The paraglossalia which provide support for the tongue itself have long posterior processes, and anteriorly they meet and run side by side to a point about one-third of the way from the tip of the tongue. The remainder of the tongue is purely corneous. The basihyal



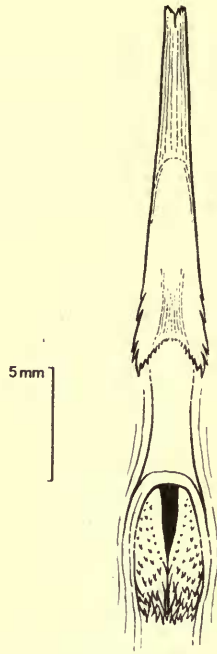


FIG. 19. *Heteralocha acutirostris* (♂ 1), tongue and larynx in dorsal view.

is a slender rod of roughly triangular section, with the apex of the triangle uppermost. The flattened urohyal, expanded at its posterior tip, and the hyoid horns (each consisting of the ceratobranchial posteriorly and epibranchial distally) are of similar form to those of many passerines.

The tongue muscles in *Heteralocha* show few unusual features, and no significant sexual dimorphism was encountered in the dissections. The descriptions given are therefore brief ones; illustrations are given in Figs. 21 and 22. More detailed accounts and background information are given in the general review by George and Berger (1966) and the paper on passerine tongue muscles by Engels (1938). A very full description of the tongue muscles of a single passerine species is that by Bock (1972) for the extinct *Ciridops anna* (Drepanididae). For discussions on function, reference may also be made to the account of wader tongue muscles by Burton (1974).

#### *M. mylohyoideus*

A thin muscular sheet with a long narrow origin on the medial side of the mandibular ramus, inserting on a median raphe. *M. mylohyoideus* lies ventral to the tongue and all the muscles attached to it.

#### *M. serpihyoideus*

Origin is on the occipital plate, medial to the exoccipital process (Bock, 1960b, p. 38) and insertion is on a median raphe continuous with that of *M. mylohyoideus*.

*M. genioglossus*

A narrow, strap-like muscle whose origin is from the posterior edge of the mandibular symphysis. The left and right muscles lie side by side near the origin and then diverge, running along the ventral side of the mucosa of the floor of the buccal cavity, on either side of the position of the tongue. In the region of the basihyal, the fibres of the muscle fan out to insert on the connective tissue and mucosa overlying the basihyal and its musculature, and, anteriorly, on the posterior process of the paraglossa.

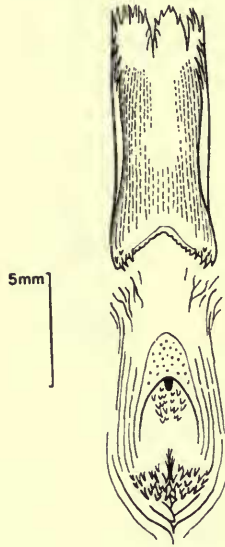


FIG. 20. *Callaeas cinerea*, tongue and larynx in dorsal view.

*M. stylohyoideus*

A long, narrow muscle originating on the ventral edge of the base of the retro-articular process, and running along the anterior edge of *M. serpihyoideus*, to insert on the lateral surface of the basihyal, just anterior to *M. thyreohyoideus*.

*M. branchiomandibularis* (= *M. geniohyoideus* of many authors)

A bulky muscle whose origin is on the medial surface of the mandible, ventral to that of *M. mylohyoideus*. A broad anterior and narrow posterior position can be distinguished. The two run parallel to insert on the hyoid horn. The anterior portion meets the horn from the ventral side, and is twisted around it for some distance before inserting on the epibranchial. The posterior portion meets the anterior on the dorso-medial side, and merges with it.

*M. ceratohyoideus*

A thin, weakly developed muscle which was found only in ♂ 1. It originates on the hyoid horn, on the ventral lateral surface of the distal tip of the ceratobranchial,

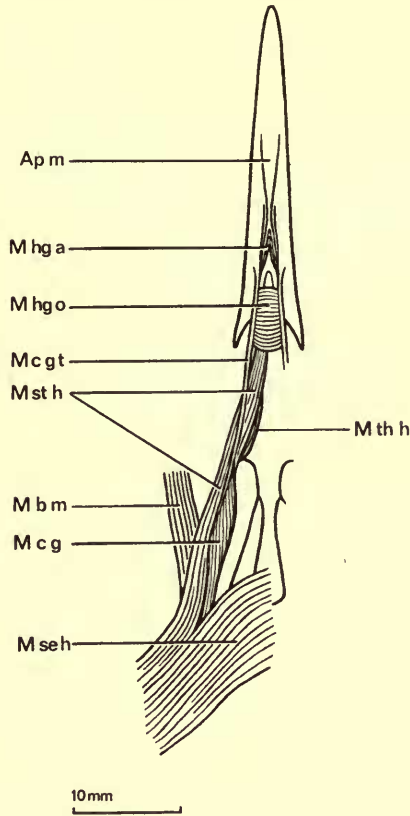


FIG. 21. *Heteralocha acutirostris* (♀ B), tongue muscles in ventral view.  
For abbreviations see p. 47.

deep to *M. ceratoglossus*. The insertion is on a median raphe continuous with that of *M. serpihyoideus* and *M. mylohyoideus*, near the posterior end of the urohyal.

#### *M. ceratoglossus*

A unipinnate muscle whose fibres arise on the surface of the ceratobranchial, and the anterior end of the epibranchial, and insert on a long lateral tendon which is itself inserted on the ventral surface of the paraglossal, just level with the anterior tip of the basihyal. No fibres insert on the tendon over the region lying alongside the basihyal, but just anterior to its attachment to the paraglossal, a small fleshy slip arises. It merges with that from the other side, and together they insert on a strong medial aponeurosis which runs along the ventral side of the paraglossalia, and inserts on the corneous anterior part of the tongue. This slip is referred to by Bock (1972 and MS) as *M. hypoglossus anterior*. A similar slip in shorebirds was described by Burton (1974) as *M. ceratoglossus anterior*; the term '*M. hypoglossus anterior*' is used by Burton (1974) to refer to a quite distinct muscle, apparently absent from

passerines, arising on the posterior tip of the paraglossals and also inserting on the median aponeurosis.

*M. hypoglossus obliquus*

Origin is on the postero-lateral process of the paraglossa. The right and left muscles are merged, the whole forming a bulky loop passing ventral to the anterior third of the basihyal.

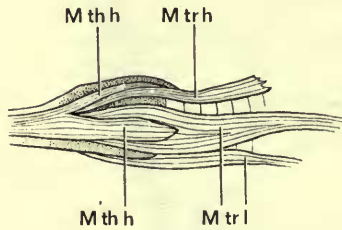


FIG. 22. *Heteralocha acutirostris* (♀ C), ventro-lateral view of tongue muscles attached to the cricoid cartilage. Cricoid and urohyal shown stippled. Both left and right Mm. tracheolateralis are visible. For abbreviations see p. 47.

*M. tracheohyoideus*

Origin is from the skin of the neck, and insertion on the lateral surface of the cricoid, just below the dorsal origin of *M. thyrohyoideus*.

*M. tracheolateralis*

The muscle originates on the syrinx, and passes along the side of the trachea, broadening anteriorly to insert by two heads on the lateral surface of the cricoid.

*M. thyrohyoideus*

This muscle originates from the lateral surface of the cricoid, by a dorsal and a ventral slip. The dorsal one is slender, and is attached just below the dorsal edge of the cricoid. The ventral slip is broader, and arises between the two heads of insertion of *M. tracheolateralis*. These slips unite anterior to the larynx and insert on the anterior lateral surface of the basihyal posterior to the insertion of the more slender *M. stylohyoideus*.

*M. ceratoglossus superior* (Bock, 1972) was not found in *Heteralocha*. The glottal muscles (*M. thyroarytenoideus* and *M. constrictor glottidis*) conform to Bock's description for *Ciridops anna*.

VII. NECK AND NECK MUSCULATURE

The thorough review by Boas (1929) has provided the basis for most subsequent studies of the avian neck and its musculature. Boas concentrated on non-passerines, principally large species, but detailed information on several small passerines is given by Palmgren (1949). There is, however, little information on the cervical

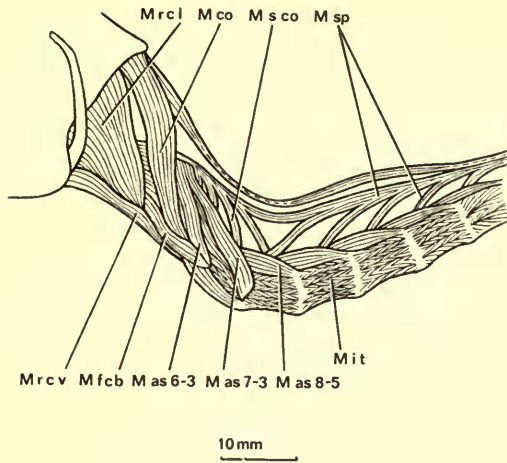


FIG. 23. *Heteralocha acutirostris* (♀ C), lateral view of superficial neck muscles.  
For abbreviations see p. 47.

muscles of larger passerines comparable in size with the Callaeidae. The majority of neck muscles perform several actions which interact in a complex way, and their individual functions are omitted from the present account in the interest of brevity. Reference may be made to Boas and Palmgren, and to the excellent discussions on neck muscle function by Zusi (1962, 1969).

There are 14 cervical vertebrae in *Heteralocha*, as in most passerines. This total includes the two cervico-dorsal vertebrae (13 and 14) which bear movable ribs not articulating with the sternum, but from a functional standpoint are best treated with the neck. The rib on 13 is extremely short, while that on 14 is long, almost reaching the sternum, but lacking an uncinat process. Six pairs of ribs actually articulate with the sternum, as in *Corcorax*, but unlike most passerines which only have 5 ribs attached to the sternum (Beddard, 1898).

Boas showed that the neck of birds consists of three sections, distinguishable by both functional and morphological differences. Section I, the most anterior, can only be flexed downward, and Section II only upward. Section III can be flexed downward, and also upward at its anterior end. In *Heteralocha*, the constitution of the segments agrees with Palmgren's division for smaller passerines (although Palmgren omitted the cervico-dorsal vertebrae from his count). The division is as follows: Section I, vertebrae 1 to 4; Section II, vertebrae 5 to 9; Section III, vertebrae 10 to 14. The vertebrae of Section I (except the atlas) have strong neural spines and hypapophyses. Those in Section II lack neural spines (except for a weak one on 5) and have no hypapophyses; they are more elongated than the vertebrae of Sections I and III. The vertebrae of Section III have hypapophyses; that on 10 is weak, but they increase in size posteriorly. The last, and largest, hypapophysis is on 15, the first dorsal vertebra. Vertebra 14 has a strong neural spine.

The account below follows the same order and terminology as Palmgren, with modification in the case of Mm. splenii accessorii and Mm. intercristales.

*M. biventer*

This muscle arises from the dorsal surface of the aponeurosis of origin of *M. spinalis* in the region of 13, and inserts on the dorsomedial edge of the occipital deep to *M. complexus*. The muscle consists of two fleshy bellies linked by a flat tendon extending approximately from 8 to 5. Little variation was encountered.

*M. spinalis*

The muscle consists of a series of fleshy slips from the ventral surface of an aponeurosis attached to the neural spines of vertebrae 14 to 18. These insert on the anapophyses of 2 and of 5 or 6 to 13; the most posterior of these is feeble and indistinct in most of the specimens. Variations in the specimens of *Heteralocha* were as follows:

Slips to both 5 and 6 present: ♀ A, ♀ B.

Slip to 6 present, slip to 5 absent: ♂ 1, ♂ 3, ♀ C.

Slip to 5 present, slip to 6 absent: ♂ 2.

*Mm. splenii colli*

These muscles are a series of slips arising from the lateral surfaces of the neural spines of 3 or 4 successive vertebrae, and joining the most anterior slip of *M. spinalis* which inserts on 2. The vertebrae of origin in the *Heteralocha* specimens are:

4 to 7: ♂ 1, ♀'s A, B and C.

4 to 6: ♂ 2, ♂ 3.

*Mm. splenii accessorii and Mm. intercrustales*

In order to clarify the relationships between these two rather similar groups of muscles it seems desirable to deal with them together. The muscles included under these headings in *Heteralocha* are as follows:

a. A muscle running from the anterior surface of the neural spine of 14 to the transverse-oblique crest of 13, and a similar muscle connecting 13 and 12.

b. A series of muscles connecting the transverse-oblique crests of successive vertebrae from 13-12 to 6-5.

c. Muscles arising on the ventro-lateral surfaces of the neural spines of 5 to 3 and inserting on the transverse-oblique crests of 4 to 2.

d. A muscle arising on the dorso-lateral surface of the neural spine of 3 and inserting on the anapophysis of 2, and a similar but weaker muscle arising on the neural spine and medial part of the neural arch of 2 and inserting on the anapophysis of 1. That arising on 3 closely resembles *Mm. splenii colli*.

e. A narrow, flat slip arising from the ventral part of the neural spine of 5 and inserting on the anapophysis of 3, somewhat resembling *Mm. dorsales pygmaei*.

According to Palmgren's criteria, groups *a* and *b* only should be regarded as comprising the *Mm. intercrustales*, and groups *c*, *d* and *e* should be treated as *Mm. splenii accessorii*. (In the small species examined by Palmgren the two muscles running antero-laterally from the neural spine of 3 are inseparable.) However, it would seem more consistent with Boas's work to include group *c* also in *Mm. intercrustales*, and to reserve the term *Mm. splenii accessorii* for groups *d* and *e*.

No noteworthy variations between individuals were found.

### *M. splenius capitis*

This muscle originates from the neural spine of 2 and inserts on the posterior surface of the skull deep to *M. complexus* and *M. biventer cervicis*. No variations in siting were found, and there is little indication of cruciform structure (Burton, 1971a).

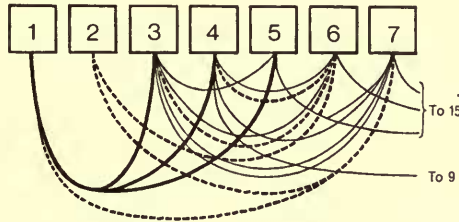


FIG. 24. Diagram to show arrangement of slips of some ventral muscles in the anterior part of the neck in *Heteralocha acutirostris* (♀ B). Heavy lines = *M. flexor colli brevis*. Broken lines = *M. flexor colli profundus*. Fine lines = anterior slips of *M. longus colli ventralis*.

### *Mm. pygmaei*

Origin is from the medial region of the neural arches of 12 to 8. Each muscle inserts on the lateral edges of the transverse-oblique crest of the second vertebra anterior to it except that from 12 which inserts on 11. The latter muscle is weak in most of the specimens and absent in ♂ 1.

### *Mm. interspinales*

These three muscles connect the well-developed neural spines of 2, 3, 4 and 5, and were present in all specimens examined.

### *Mm. ascendentes cervicis*

These muscles arise on the diapophyses of cervical vertebrae up to and including 6. Most consist of two slips inserting on the anapophyses of the second and third vertebrae anterior. That from 7 consists of three slips inserting on 3, 4 and 5 in all specimens, and that from 8 sends an additional slip to 4 in ♂'s 1 and 2. The short slips arising on 12 and posteriorly are relatively weak, and also showed some minor variations in siting. The series is continued posteriorly as *Mm. ascendentes thoracis*, but those arising posterior to 14 were not dissected.

### *Mm. intertransversarii*

These laterally situated muscles connect successive vertebrae. The most anterior are those from 3 to 2, and the most posterior those from 13 to 12. Each muscle arises from the anterior surface of the transverse process and inserts on the posterior surface of the transverse process of the vertebra in front; that from 4 to 3 inserts on

the medial surface of the rib of 3, and that from 3 to 2 inserts on the lateral surface of the centrum of 2.

As far as 6-5, the *Mm. inclusi* lie deep to *Mm. intertransversarii*, and closely associated with them. Palmgren regards the muscles anterior to this as continuing the series of *Mm. inclusi*; Boas and Zusi treat them with *Mm. intertransversarii* as is done here.

The *Mm. intertransversarii* are multipinnate muscles, traversed by interdigitating raphes from origin and insertion. The muscles are bulkiest and the number of raphes greatest in the region from 7 to 10. Up to 9 raphes have been detected in 9-8 or in 10-9, the number and situation of raphes showing small individual variations. The muscle connecting 13 and 12 is reduced to a small dorsal slip, while those anterior to 5 are also of small size.

#### *Mm. inclusi*

These muscles are concealed by *Mm. intertransversarii*, and can only be separated from them with difficulty. Each one arises on the anterior surface of the transverse process medial to *M. intertransversarius*, and inserts on the lateral surfaces of the neural arch and centrum of the next vertebra in front. Most show division into dorsal and ventral bellies (*Mm. inclusi superiores* and *inferiores*). In the most posterior two (12 to 11 and 11 to 10), only *inferiores* can be distinguished. The most anterior are those connecting 5 and 6.

#### *M. longus colli ventralis*

This complex muscle consists of a series of fleshy slips arising on the sublateral processes, hypapophyses and anterior part of the centra of vertebrae 15 to 6. The main part of the muscle inserts by a series of 7 tendons on the ribs of 11 to 5. Each vertebra sends a slip to join each of the tendons traversing it; there are thus 7 such slips from each of vertebrae 15 to 12 after which the number of slips decreases by one for each vertebra anterior to this. In the region 15 to 12 the slips are densely crowded and difficult to separate and some of the deepest fibres appear to attach to adjacent vertebrae.

A smaller group of slips situated anteriorly is also included with *M. longus colli*. Three of these arise from a tendon attached to the sublateral process of 7, which also provides origin for part of *M. flexor colli profundus*. They insert on ribs 3 and 4 by short aponeuroses and on the long tendon attached to rib 5. Slips also arise on the ventral anterior surfaces of the lateral processes of 7, 6 and 5, the two former in close association with the *Mm. intertransversarii*, and immediately below them. These attach on rib 3, and those from 6 and 7 also on rib 4; minor variations occur. Two slips arise from the sublateral process of 6 and insert on ribs 3 and 4, and there is also a longer slip arising on 9 (8 in ♀ C) which inserts by a weak tendon on rib 4. This tendon also appears to receive some fibres from the posterior part of the muscle.

#### *M. flexor colli brevis*

Lateral and medial parts may be distinguished in this muscle. The lateral part constitutes the greater bulk of the muscle and originates from the ventral surface



of the lateral strut of 3 ; and from the lateral processes of 4 and 5 in the ♀'s and 6 also in the ♂'s. The medial portion is separated from the lateral by the anterior part of M. longus colli ; it takes origin from the sublateral processes of 3, 4 and 5.

The lateral and medial portions join anterior to rib 3 and insert by a tendon on the postero-ventral processes of the centrum of the atlas.

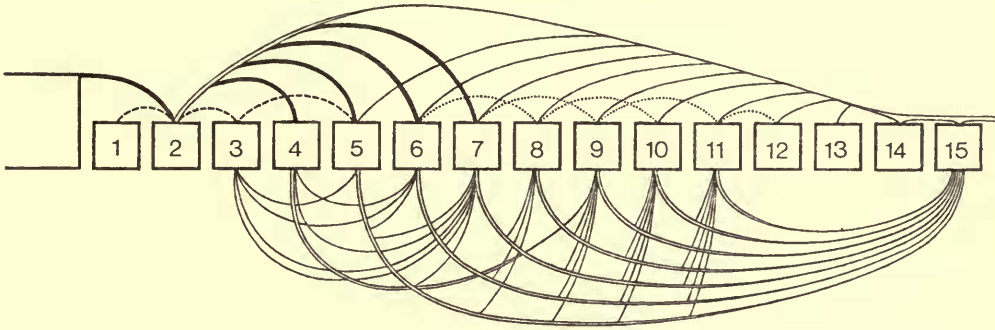


FIG. 25. Diagram to show arrangements of slips of some neck muscles in *Heteralocha acutirostris* (♀ A or ♀ B). Heavy lines = M. splenius capitis and Mm. splenii colli. Fine lines = M. spinalis (dorsal) and M. longus colli ventralis (ventral). Broken lines = Mm. splenii accessorii (as defined in text). Dotted lines = Mm. pygmaei. Tendons of M. spinalis and M. longus colli ventralis are represented by double lines.

#### *M. flexor colli profundus*

Origin is from the sublateral processes of 4, 5, 6 and 7. The slips from 4 and 5 arise immediately deep to the medial portion of M. flexor colli brevis and insert on the hypapophysis of 2. From 6, slips run to insert on the hypapophyses of 2, 3 and 4 (♂ 2, ♂ 3, ♀ B) or of 3 and 4 only (♂ 1, ♀ A, ♀ C). From 7 a long slip runs to the hypapophysis of 2 ; this slip shares a tendinous origin with the medial slip of M. longus colli from 7 to 3. In ♂ 2, ♂ 3 and ♀ B the slip bifurcates and a branch continues forwards to fuse with M. flexor colli brevis near its insertion. The slips arising on 6 show some fusion with M. rectus capitis ventralis at the origin.

#### *M. complexus*

Origin is from the lateral strut of 4, the diapophysis of 5, and from an aponeurosis attached to the diapophysis of 6. Insertion is on the dorsal edge of the occipitals.

#### *M. rectus capitis lateralis*

Origin is from the hypapophyses of 2, 3 and 4, and insertion on the lateral dorsal edge of the exoccipital.

#### *M. rectus capitis superior*

This muscle lies immediately superficial to M. flexor colli brevis. Origin is from the lateral surface of neural arch 1, from the anterior surfaces of anapophyses 2 and

3, from the lateral strut of 4, and from the transverse processes of 5 and 6. Origin from 6 is absent in all the female specimens and in ♂ 2; origin from 5 is also absent in ♀ C. Insertion is aponeurotic and fleshy on a ridge at the posterior edge of the basitemporal plate.

*M. rectus capitis ventralis*

Origin is from the ventral surface of 1, from the hyapophyses of 2, 3, 4 and 5, and from the sublateral process of 6 where there is some fusion with *M. flexor colli profundus*. The right and left *Mm. recti capiti ventrales* are fused in the midline and insert together on the basitemporal plate, anterior to *M. rectus capitis superior*.

VIII. OTHER CALLAEIDAE

*Creadion carunculatus*

The description of the Huia's skull by Oliver (in Phillipps, 1963) refers to the general similarity of the skull of *Creadion*. Oliver notes the greater extent of ossification in *Heteralocha*, manifested especially at the front of the orbit. The skull and skeleton of this species are figured by Shufeldt (1913), who includes some brief notes on its skull for comparison with *Anthochaera carunculata* (Meliphagidae).

The following additional points may be noted. The retroarticular process is highly developed in *Creadion*, but is nevertheless relatively shorter than that of the Huia; there is no raised occipital crest, and little development of an exoccipital process. Otherwise, skull proportions are similar to *Heteralocha*, particularly female specimens, though the quadrate and pterygoid are relatively smaller. The skull is apparently larger relative to body size in the Saddleback if a rough index (sternum length) from a single specimen can be relied upon. Ligaments have been removed from the skull of the available specimen, and could not be studied.

With the exception of *M. depressor mandibulae*, jaw muscles have also been removed from the specimen of *Creadion*. This remaining muscle is, however, of considerable interest, since it possesses a pars anterior as in *Heteralocha* – a feature which otherwise appears to be unique among birds so far studied. The rest of the muscle is also well developed, and similar in structure to that of the Huia, though relatively less massive. The tongue, like the jaws, is smaller relative to the skull in *Creadion*, but the hyoid musculature is closely similar in both Saddleback and Huia.

Due to the historic interest of the specimen, only limited dissection of the neck muscles could be undertaken for *Creadion*. Five of the muscles exhibiting variation in the Huia or among other passerines were examined. These showed an overall reduction in the number of sites of attachment. *M. spinalis* lacks the slip inserting on 5 which is present in three of the Huia specimens, though a slip to 6 (absent in Huia ♂ 2) is present. *M. splenius colli* lacks the slip to 7 found in four of the Huia specimens. *M. flexor colli brevis* and *M. rectus capitis superior* lack attachment to 6, a feature found in three and two of the male Huia specimens respectively. *M. complexus* also lacks a slip to 6, although this is present in all six Huia specimens dissected.

*Callaeas cinerea*

The skull and other features of the skeleton in the Kokako have been described in some detail by Stonor (1942). It is sufficient here to draw attention to the extensive differences in skull proportions and geometry between this bird, on the one hand, and *Heteralocha* and *Creadion*, on the other. The bill is shorter, but much deeper, and the jugal bar meets it at a greater angle. The quadrate is relatively much larger, and is rotated backwards by comparison with the other Callaeidae, so that its otic process meets the lower jaw more nearly at right angles. The cranium is shortened, and smaller relative to the orbits; the jugal is very long relative to the skull. The lower jaw is deep, and bears strong cristae for the attachment of the adductor musculature. There is no retroarticular process, and the articular is extremely shallow at its articulation with the quadrate. The prominent sesamoids at this articulation were noted by Stonor, and their origin and functions are discussed in detail by Burton (1973). As in the Huia, the external jugomandibular ligament is absent. The occipitomandibular ligament is not ossified at all.

The jaw musculature is notable for the highly developed adductor musculature, and the very small M. depressor by comparison with the other Callaeidae. M. adductor mandibulae externus is considerably more bulky in actual (as well as relative) size than in *Heteralocha*, with increased number of fibres and greater complexity. Its aponeuroses are generally stouter, and more branched and subdivided internally (Fig. 18), providing extra surface for fibre attachment, and consequently a greater use of pinnate structure. M. pseudotemporalis superficialis is also much larger than in the Huia and Saddleback, and in dorsal view completely conceals M. pseudotemporalis profundus, which is much reduced – a consequence of the backward displacement of the quadrate. M. pterygoideus is bulky and the retractor palatini slip is especially well developed, and prominent in dorsal view. M. depressor mandibulae is not only smaller than in the other Callaeidae, but structurally simpler, and entirely lacks a pars anterior. It is unique, however, for the pulley arrangement between its aponeurosis and the internal jugo-mandibular ligament (Burton, 1973).

The tongue is much broader relative to its length than in the Huia and Saddleback; its shape is almost rectangular, and the tip brush-like. The paraglossa which support it are widely separated. There is no median aponeurosis and M. ceratoglossus anterior is absent; otherwise, the hyoid musculature resembles that of the other two genera of Callaeidae. The palate is provided with horny papillae similar to those of the other Callaeidae, but the horny lining of both jaws is developed near the bill tip into raised, papillate bosses. There is a pair of Gll. angularis oris, but a Gl. palatinae has not been found.

Neck muscles showing variation in their points of attachment in *Heteralocha* or other passerines were examined in *Callaeas*. The two specimens dissected had the same number and sites of attachment points for the muscles examined. Slips or muscle components absent in some Huia specimens, but present in the Kokako specimens, were the insertions of M. spinalis cervicis on 5 and 6; M. splenius colli arising from 7; M. intercristalis from 5 to 3; the slip of M. ascendens from 8 to 4; and the slip of M. flexor colli brevis to 6. No Mm. pygmaei arise from 12, though this site is occupied in all but one male Huia specimen. However, an additional M.

pygmaeus from 7 to 6 is present in the Kokako specimens, though absent in all the Huias dissected. The Kokakos lacked the slip of *M. flexor colli profundus* from 6 to 2, present in three of the Huias, and the slip of *M. complexus* to 6, present in all the Huias. *M. flexor colli brevis* in the *Callaeas* specimens lacks the slip to 6 present in two male Huias, but has a slip to 5 (unlike *Creadion* and one female Huia specimen).

## IX. FUNCTIONAL ASPECTS

### *Jaw mechanism*

Next to the form and sexual dimorphism of the bill, the most striking features of the Huia's cranial morphology are the huge *M. depressor mandibulae* and associated skull modifications – the prominent occipital crest, providing extra surface for its origin, and the very long retroarticular process providing increased leverage for the muscle. Clearly these adaptations must permit the lower jaw to be depressed with great force. This can only be necessary if it is to be opened against considerable resistance by external forces, and it seems certain, therefore, that the Huia was highly specialized for feeding by 'gaping' or 'prying'. This feeding technique consists basically of thrusting the bill into a potentially food-bearing medium (earth, wood, fruit, etc.) and opening it, to widen the hole and so facilitate exploration or prey extraction.

Gaping is a technique described from birds of several families. Among passerines, good examples are furnished by some Sturnidae and many Icteridae. Gaping behaviour and related modifications of *M. depressor mandibulae* have been studied in the Icteridae by Beecher (1951). It is interesting to compare the Huia with other birds specialized for gaping, and some figures for relative length of the retroarticular process in several examples, mainly of passerines, are given in Table 2. The nearest approach is shown by *Cacicus solitarius* in which the retroarticular process is slightly longer relative to the lower jaw than in the Huia. However, *Cacicus solitarius* is a shorter billed bird; relative to skull length, its retroarticular process is shorter than in *Heteralocha*, a difference which would be even greater but for the Huia's elongated skull with enlarged occipital crest. It seems clear that the Huia was very highly specialized for feeding by gaping, perhaps more so than any bird now living.

Buller's account of the Huia's feeding behaviour is an excellent one, but clearly gives an incomplete picture of the male's excavation methods. Buller remarks that the captive male used its bill to 'chisel out' pieces of decayed wood in a woodpecker-like manner. Almost certainly its precise technique must usually have been to drive the bill into the wood and 'gape' to split portions off; this is actually quite different in principle from the methods of woodpeckers which depend purely on blows. Buller states that the female he observed fed in a quite different manner, by probing into relatively hard wood. However, *M. depressor mandibulae* and the retroarticular process, though somewhat smaller in the female, are still very large by comparison with other birds, and her capacity for forceful depression of the lower jaw must also have been very high. Due to the greater length of the female's bill, less force could be exerted at its tip than in the male; and the more flexible nature of its anterior, purely rhamphothecal, portion, appears rather inefficient for gaping.

TABLE 2

Relative length of the retroarticular process in single specimens of various birds showing gaping adaptations, and in all intact Huia specimens used in this study

	A Total length of lower jaw	B Length of retroarticular process	C Cranium length	$\frac{B}{A}$ Retroarticular Lower jaw	$\frac{B}{C}$ Retroarticular Cranium
<i>Upupa epops</i>	81.0	5.6	25.4	0.07	0.22
<i>Phoeniculus porphyreus</i>	60.4	6.2	26.3	0.10	0.24
<i>Phoeniculus aterrimus</i>	45.4	4.4	20.5	0.10	0.21
<i>Psarocolius decumanus</i>	65.2	7.8	36.9	0.12	0.21
<i>Psarocolius wagleri</i>	72.6	7.9	37.0	0.11	0.21
<i>Cacicus cela</i>	43.1	4.0	29.1	0.09	0.14
<i>Cacicus leucorhamphus</i>	48.7	5.2	29.8	0.11	0.17
<i>Cacicus solitarius</i>	53.5	10.3	31.1	0.19	0.33
<i>Sturnella magna</i>	44.2	5.5	31.3	0.12	0.17
<i>Amblyramphus holosericeus</i>	45.4	8.0	28.0	0.18	0.29
<i>Creatophora cinerea</i>	41.7	2.8	28.8	0.07	0.10
<i>Sturnus vulgaris</i>	43.9	5.0	29.4	0.11	0.17
<i>Sturnus contra</i>	49.5	4.7	27.8	0.09	0.17
<i>Heteralocha acutirostris</i> , ♂ (mean of 3)	89.4	16.4	46.8	0.18	0.35
<i>Heteralocha acutirostris</i> , ♀ (mean of 2)	109.5	13.5	43.0	0.12	0.31
<i>Pyrhacorax pyrrhacorax</i>	77.0	5.4	40.9	0.07	0.13

Nevertheless, gaping must also have been an important part of her repertoire of feeding techniques in addition to exploratory probing (as described by Buller) for which the decurved bill shape is evidently adapted. In probing timber tunnelled by beetles, it seems feasible that the bill might occasionally be inserted through a crack into a larger cavity, so that gaping could take place with contact only in the more rigid basal part of the bill. However, the possibility remains that the female's apparent gaping adaptations reflect principally the shared genotype of the two sexes (see under Sexual Dimorphism).

In addition to its large size, *M. depressor mandibulae* in the Huia also shows interesting structural complexities. A major contribution to the force of depression is obviously provided by the large mass arising posteriorly and dorsally on the cranium, since this is not only bulky, but has the longest moment arm due to its insertion near the posterior extremity of the retroarticular process. However, the

anterior parts of the muscle also exhibit various modifications. Several aponeuroses are present, serving as the basis for pinnate fibre arrangements ; this may be related to their short working distance, for which pinnate structure should provide more forceful contraction than parallel fibred muscles of the same physiological cross section (Gans and Bock, 1965). The pars anterior of the muscle (present also in *Creadion*) is of particular interest, since it appears not to have been described previously in any other bird, and was certainly absent from gaping species of other families dissected during this study. Its functions are hard to surmise, and a satisfactory explanation will probably require a much more detailed knowledge of the jaw mechanics involved in gaping than is available at present.

Except for fibres inserting on the internal process, the greater bulk of *M. depressor mandibulae* has a medial component in contraction which is greatest for the most posterior parts of the muscle originating near the midline of the cranium. The unusual prominence of the medial condyle of the quadrate may in part serve to resist the stress which this places on the quadrate/mandible articulation.

Probably *M. depressor* also aids protraction of the upper jaw by the action of its upward force component on the quadrate (see Bock, 1964, 1968, and Zusi, 1962, 1967, for discussions of this mechanism), but *M. protractor quadrati et pterygoidei* is itself well developed. It is certainly evident that upper jaw action contributes substantially to 'gaping'. The unusual situation of the nasal-frontal hinge may be relevant in this respect. Its position, more dorsal and posterior than in other passerines, places it further from the line of action of the protractor force, acting through the palatines and jugals ; the moment arm of this force is consequently increased.

The remainder of the jaw musculature, concerned with adduction of the lower jaw and depression of the upper jaw, calls for less comment. It is well developed, as seems necessary to provide sufficient grip while extracting huhu grubs, but not remarkably so ; in general features, the muscles other than *M. depressor* and *M. protractor* resemble those of *Corvus* described by Bock (MS).

### *Skull architecture*

There is a need for detailed and comparative mechanical analyses of the skull in 'gaping' passerines of a comparable depth to those available for biting and seed crushing forms, e.g. Bock (1960a, 1964b, 1966) and Bowman (1961). Here, some features of possible significance in the skull of *Heteralocha* will be briefly noted.

The wedge-shaped bill of the male Huia is typical of the majority of 'gapers' and resembles that of many Icterids. The straight-sided culmen and gonys are more efficient than the blunter, arched bill of most passerines for the task of forcing the bill into the substrate prior to gaping. Decurved bills, such as those of the female's, or some wood hoopoes (*Rhinopomastus* spp.), depend for this on the presence of existing crevices or tunnels. In the case of the wedge-shaped bill, the narrower and more acutely conical its form, the more easily it will penetrate the substrate ; a limit is imposed by the danger of damage by forces directed across the bill axis, since this hazard is less in a more broadly based cone (see Bowman, 1961, p. 222-224). Evidently this danger was not exceptionally high in the Huia, since the male's bill

is narrower and more acute than in many Icterids, including the wood-prying caci-ques ; and in both sexes, the angle between the jugal bars and mandibular rami (giving lateral support to the bill) is no greater than in many unspecialized passerines.

The culmen of the bill and frontal bridge of the skull are virtually in line, again a feature of many 'gapers', but particularly well marked in the Huia, with the nasal-frontal hinge shifted to an unusual position nearly halfway across the orbital region. This profile eliminates the difficulties that might arise with a more conventional skull possessing a marked 'forehead' at the nasal-frontal hinge if the bill were thrust into the feeding substrate up to or past its base. Many Icterids in fact have the culmen raised above the level of the frontal bridge ; the horny plate extending onto the forehead of some members of this family (e.g. *Gymnostinops*, *Psarocolius*) is probably adaptive primarily to gaping in succulent fruits (Beecher, 1951).

The stoutness of the quadrate-jugal articulation in *Heteralocha* is probably related to the great development of *M. depressor mandibulae*. The prominence of the medial condyle of the quadrate and its orientation are also unusual ; the long axis of the condyle is directed more nearly at right angles to the skull axis than in most passerines, a feature which may be adaptive to resisting backward disarticulation by strong external forces.

The nasal-frontal hinge appears to be unusually ill defined in *Heteralocha*, and manipulation of skulls relaxed by boiling suggests that the bending zone is considerably longer and stiffer than in most holorhinal birds. This may have some significance as a safety factor, since a wood 'gaper' could be exposed to some danger of over-protraction in the event of timber splitting suddenly while a strong force was still being exerted by the upper jaw. However, there are no bony protraction stops comparable to the overhanging frontal 'brow' of woodpeckers – part of a completely distinct adaptive complex based on the use of *M. protractor* to distribute compression forces while hammering (Spring, 1965, Bock, 1966).

#### *Buccal cavity, tongue and hyoid musculature*

Although the Huia's manner of gaining access to its food is specialized, the food itself (Cerambycid larvae) and the process of swallowing it pose no unusual problems. It is consequently no surprise that the papillae of the upper jaw, tongue and larynx resemble those of many other passerines which feed on invertebrate prey. The hyoid musculature is similarly unspecialized. Cerambycid larvae are smooth skinned, and would not seem to require a great deal of lubrication. The limited complement of salivary glands is consistent with this supposition.

#### *Neck musculature*

By comparison with the other two species of Callaeidae, the neck musculature of *Heteralocha* appears better developed inasmuch as several of the muscles or muscle groups occupy additional sites of origin or insertion. It is difficult, however, to draw general inferences from this, owing to the scarcity of information on other passerines. Palmgren's (1949) study, though detailed, concentrated on small species of passerines ; Boas (1929) confined his work mainly to non-passerines. In the absence of such information for larger passerines, it is not possible to know to what

extent this difference is due to the Huia's larger size. For the present it is only possible to remark that greater development of the neck musculature would be expected in a bird so highly adapted to the extraction of prey from timber by vigorous techniques.

#### *Other Callaeidae*

The Saddleback is known to excavate for insect food in decayed timber, bark, epiphytes, etc., and also takes some huhu grubs. It is clear from its skull that in this species, too, gaping must play a large part in its feeding activities. However, it is less specialized than the Huia, even apart from the lack of pronounced sexual dimorphism. Correlated with its smaller body size, it includes a larger proportion of small insects and other items in its diet, and has never reached the high degree of dependence on a single prey species seen in the Huia.

The Kokako is primarily a fruit and leaf eater. In many features of its cranial morphology it shows convergence with finches or with parrots. These features are centred around the need for powerful adduction for biting hard or tough vegetable foods. In the skull, the jaws are shortened and deepened, and the quadrate/mandible articulation shifted posteriorly. The curious structure of the mandible/quadrate articulation is evidently a consequence of these trends (Burton, 1973a). There is no retroarticular process, and it is doubtful if gaping adaptations were ever present in its ancestry. The adductor musculature is more bulky and complex than in the Huia and Saddleback, and the tongue is specialized, probably for dealing with fruits.

### X. SEXUAL DIMORPHISM

#### *Bill*

The great difference in size and shape of the bill between male and female Huia is of course well known. It does not appear to have been realized, however, to what a large extent this is due to differing development of the rhamphotheca. With the rhamphotheca removed, the bill length difference is reduced and the skulls of the two sexes resemble each other much more closely (Fig. 26). The greatly elongated rhamphotheca of the female is remarkable not only by comparison with the male, but also when compared with other birds of similar bill form. Table 3 gives figures for upper jaw length with and without rhamphotheca in specimens of a variety of birds (mainly passerines) with long decurved bills. It can be seen that all of these fall well short of the female Huia in relative development of the rhamphotheca, and some bills of very extreme form are bony right to the tip. It is difficult to assess the significance of this feature. From a functional viewpoint, it might be suggested that the relatively flexible material of the rhamphotheca would be in less danger of breakage than bone when used for vigorous exploration of timber.

However, developmental and genetic factors should also be taken into consideration. The greater development of the rhamphotheca in the female may be a special case of allometric growth; this might be investigated by soft x-ray photography of the fairly extensive series of Huia skins in the world's museums. It is also possible



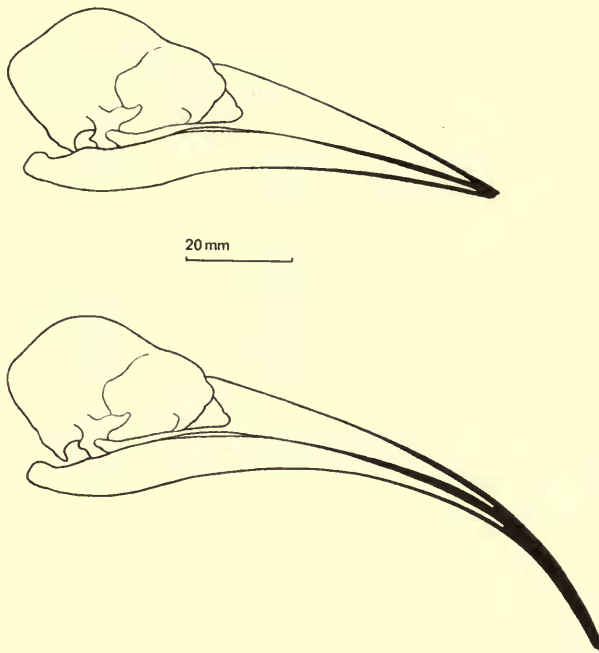


FIG. 26. Comparative development of the rhamphotheca in male and female of *Heteralocha acutirostris* (♂ 1 and ♀ C). Solid black areas represent the profile of the rhamphotheca.

that the answer may lie in the differences between the genetic control of development of rhamphotheca and of bone; it may simply be 'easier', genetically, to evolve extreme sexual dimorphism of bill length in this way. Other examples of this phenomenon may exist. For example, the lark *Alauda razae* shows marked sexual dimorphism in bill length (Burton, 1971b) and soft x-ray photographs of three specimens of each sex show proportionately greater rhamphothecal development in the longer-billed males. Investigation of longer series of this and other sexually dimorphic species may shed further light on this problem.

Close examination of Huia specimens showing features intermediate between male and female (e.g. some specimens mentioned by Phillipps, 1963) also seems desirable. It may be mentioned in passing that the male specimen figured by Garrod (1872) seems to have been unusual in this respect. Garrod mentions that its tongue was a third the length of the bill. Assuming the tongue was of normal length, this would mean a bill some 90 mm long, a length normally found only in females. The figures show other unusual features; the jaw tips are attenuated and slightly decurved, rather as in female specimens, and the occipital crest is less prominent than in the males examined in this study. On the other hand, bill depth and stoutness of the jugal, palatines and pterygoids are characteristically male. The specimen was acquired by the Zoological Society of London nearly two years before its death

TABLE 3

Extension of rhamphotheca beyond upper jaw tip in single specimens of various birds with long downcurved bills, and in male and female *Huia* specimens used in this study

	A Upper jaw from junction of nasal and jugal bars, rhamphotheca intact	B Upper jaw from junction of nasal and jugal bars, rhamphotheca intact	$\frac{A-B}{A}$ Relative length of rhamphothecal extension
<i>Upupa epops</i>	63.5	52.3	0.18
<i>Rhinopomastus cyanomelas</i>	37.7	33.0	0.12
<i>Campylorhamphus trochilirostris</i>	62.0	55.5	0.10
<i>Falcula palliata</i>	66.7	58.5	0.12
<i>Nectarinia famosa</i>	35.2	30.8	0.13
<i>Arachnothera robusta</i>	54.9	53.9	0.02
<i>Hemignathus procerus</i>	60.6	46.8	0.23
<i>Heteralocha acutirostris</i> , ♂ (mean of 3)	50.2	43.5	0.10
<i>Heteralocha acutirostris</i> , ♀ (mean of 2)	90.5	49.7	0.45

(Zoological Society of London, 1870); possibly it was young when acquired, and developed abnormally in captivity.

### *Jaw mechanism*

*M. depressor mandibulae* is of essentially similar structure in both sexes, but distinctly less massive in the female. Differences in skull features associated with this are the less prominent occipital crest (and consequently shorter skull), and shorter exoccipital and retroarticular processes of the female.

Comparisons between male and female for the other jaw muscles are of very limited value, since these remain in only one female specimen (♀ C). In this specimen, *M. adductor mandibulae externus* appears distinctly more bulky than in the three males, although the medial slip of *M.a.m.e. rostralis medialis* is shorter. Greater development of this muscle would seem reasonable in view of the female's greater bill length, a consequence of which would be to reduce the mechanical advantage of the muscle for bill tip adduction – an action which might require considerable force when gripping and extracting huhu grubs.

### *Skull*

Features related to differences in bill form and in development of *M. depressor mandibulae* have already been mentioned. Apart from these, the proportions of the

skull are very similar in both sexes, as can be seen from Table 1. The only significant difference in proportion is in the region of the bill base. In the female, the bill is relatively narrower and less deep at the base, and the skull is narrower anterior to the orbits. Probably her mode of feeding involved less exposure to forces directed across the bill axis than the more vigorous techniques of the male. Ratios of jugal length to sternum length give no indication of any difference between the sexes in relative head size.

#### *Buccal cavity, tongue and tongue musculature*

Despite the much greater length of the female's bill, the tongue is of similar size in both sexes. It would have been of little use for the extraction of prey by the female, and in both sexes was probably concerned simply with manœuvring food during the process of swallowing. It is therefore not surprising that the hyoid musculature shows no obvious sign of sexual dimorphism. The same is true also of the buccal papillae and salivary glands, whose functions would have been similar in both sexes.

#### *Neck musculature*

Several of the neck muscles and muscle groups showed variations in the number and disposition of components. Table 4 compares the distribution of these variable components in the three spirit specimens of each sex, and a fairly clear pattern emerges. Variable slips and components of the dorsal muscles (concerned mainly

TABLE 4

Distribution of neck muscle components present in some, but not all, of the Huia specimens

	Number of specimens in which present		
	Male	Female	TOTAL
<b>Dorsal components</b>			
M. spinalis insertion on 5	1	2	3
M. spinalis insertion on 6	2	3	5
M. splenius colli origin on 7	1	3	4
M. pygmaeus from 12 to 11	2	3	5
M. ascendens from 8 to 4	2	0	2
	—	—	—
TOTAL	8	11	19
<b>Ventral components</b>			
M. flexor colli profundus from 6 to 2	2	1	3
M. flexor colli profundus slip joining			
M. flexor colli brevis	2	1	3
M. flexor colli brevis origin from 6	3	0	3
M. rectus capitis superior origin from 5	3	2	5
M. rectus capitis superior origin from 6	2	0	2
	—	—	—
TOTAL	12	4	16

with raising the neck) are slightly better represented in the female specimens. However, a much greater disparity exists among the variable components of the ventral muscles (concerned with lowering the head and neck), which are much better represented in the male specimens.

This discrepancy is entirely consistent with the difference between the feeding methods of male and female. Forceful downward movements of head and neck must have been essential to enable the male to insert his bill into timber before 'gaping' to split it; this would have been much less important in the female who relied on the presence of existing tunnels and crevices into which to insert her bill. The preponderance of variable components of the dorsal musculature in the female is less extreme, but may also correspond to a difference in use. Extracting huhu grubs must have entailed exertion in lifting the head and neck for both sexes; but this exertion may often have been greater for the female, since a larger proportion of her prey would have to be removed from more or less intact tunnels due to the harder wood in which she fed and her lower capacity for forceful 'gaping'.

#### XI. CONCLUDING REMARKS

Several studies of the Huia's morphology have been undertaken in attempts to clarify its systematic position. I would be reluctant, however, to draw any conclusions about the Huia's affinities from the results of the present investigation. Most of the foregoing descriptions and discussions have been centred around the extremes of sexual dimorphism and adaptation for gaping shown by the Huia, but neither phenomenon is unique among passerines except in degree. Indeed several of the features to which Garrod (1872) gave greatest weight in allying *Heteralocha* with the Sturnidae were gaping adaptations and the genera of 'Sturnidae' which he examined included several New World forms now assigned to the quite distinct family Icteridae. Firstly, the size of *M. depressor mandibulae* (the 'digastric' muscle) which impressed Garrod and also Lowe (1938) with its similarity to various Sturnidae is an unsatisfactory character unless considered in conjunction with the structure of the muscle. In this respect, *Heteralocha* and *Creadion* both show a feature which is apparently unique – a pars anterior, extending forwards from the articulation with the quadrate. Secondly, *Callaeas*, an undoubted relative (Stonor, 1942) of these two genera, shows no gaping adaptations, and quite possibly did not evolve from a gaping ancestor. It seems reasonable to suggest that the gaping adaptations of the Huia and Saddleback evolved independently of other families and in isolation, and if this is correct, they are poor evidence for affinity with other gaping forms.

The details revealed by this study do not, either, affect the general conclusion of Selander (1966) that extreme sexual dimorphism in feeding structures is particularly frequent in insular bird species, since it provides a means of utilizing a wider range of food resources in conditions of reduced competition. However, the dimorphism of the bill in the Huia is the most extreme example known of this phenomenon, and it is natural to wonder how such a large difference between the sexes evolved. The gaping adaptations may well have played a crucial part. Gaping is an unusual means

of exploiting the food resources of timber, and among passerines in general, probing is a much more common technique. Nevertheless, gaping was almost certainly the primary adaptation in the stock from which the Huia arose. The existence of similar adaptations in both sexes of the Saddleback lends strong support to this presumption. If so, the female Huia's bill form appears to be a secondary adaptation for probing, probably evolved from what was initially a slightly more slender (and very likely shorter) bill than that of the male. An early appearance of a sexual difference in feeding technique would be essential for this to take place. It should be stressed here that Buller's account gives no evidence for cooperation between the two sexes in feeding, although the terms in which it is couched appear to suggest this and have often been interpreted in this way. Almost certainly each simply fed independently in the manner for which it was adapted. The female probably derived occasional benefit from the excavations of the male, but the reasons for the Huia's regular association in pairs may primarily have been social or sexual.

Assuming the Huia to be extinct, a full understanding of the significance of its dimorphism may never be achieved. However, there are still various lines of investigation which might profitably be pursued. Further use could be made of the existing material of *Heteralocha*. In addition to the 119 New Zealand specimens examined by Phillipps (1963), several museums in other parts of the world hold series of skins. Examination of all this scattered material may prove difficult, but it would seem desirable to have the fullest available quantitative data on the extent of dimorphism and of variation within each sex. The data so far available suggest that the female's bill may have been more variable than the male's. If true, this might indicate that females obtained food in a greater variety of situations or by more versatile techniques than males (although Phillipps suggests that the male ate a greater proportion of insects other than huhu grubs). It certainly appears that the pair bond was very strong in the Huia, and that both sexes participated in feeding the young.

Studies of the Saddleback may provide information from which inferences about the Huia's behaviour can be drawn, and investigations on its feeding ecology and functional anatomy are currently in progress (Jenkins, pers. comm.). Finally, studies on other timber-feeding birds may shed further light on the Huia's adaptations. The closest parallels to these appear to be shown not by passerines, but by the Wood Hoopoes (Order Coraciiformes, family Phoeniculidae). Within this family, the genus *Phoeniculus* (particularly *P. aterrimus*) appears to parallel the male Huia, while *Rhinopomastus* spp. resemble the female, both genera showing well-marked gaping adaptations. A study of feeding behaviour and anatomy in this family, as well as being worth while in its own right, would make an interesting comparison with the Huia, in which similar bill forms and feeding methods have evolved in the two sexes of a single species.

Yet, finally, it must be admitted that these indirect methods of investigation are a very poor substitute for observations on the living bird. A study of this species in life might have provided much information of general importance for evolutionary biology, and would certainly have been of intense interest; its loss is a matter for the greatest regret.

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## KEY TO ABBREVIATIONS IN FIGURES

Ap 1 a m e	Aponeurosis 1, M. adductor mandibulae externus
Ap 2 a m e	Aponeurosis 2, M. adductor mandibulae externus
Ap 3 a d m	Aponeurosis 3a, M. depressor mandibulae
Ap m	Median aponeurosis of tongue
C o	Occipital crest
E u s	Opening of Eustachian tube
G a o	Gl. angularis oris
L i j m	Internal jugomandibular ligament
L p o	Postorbital ligament
M a m e c	M. adductor mandibulae externus caudalis
M a m e r l	M. adductor mandibulae externus rostralis lateralis
M a m e r m	M. adductor mandibulae externus rostralis medialis
M a m e r t	M. adductor mandibulae externus rostralis temporalis
M a m e v	M. adductor mandibulae externus ventralis
M a m p	M. adductor mandibulae posterior
M a s	M. ascendens cervicis.
M b m	M. branchiomandibularis
M c g	M. ceratoglossus
M c g t	Tendon of M. ceratoglossus
M c o	M. complexus
M d m	M. depressor mandibulae
M d m a	M. depressor mandibulae pars anterior
M d t	M. dermatotemporalis
M f c b	M. flexor colli brevis
M h g a	M. hypoglossus anterior
M h g o	M. hypoglossus obliquus
M i t	M. intertransversarius
M p q 1	M. protractor quadrati et pterygoidei 1
M p q 2	M. protractor quadrati et pterygoidei 2
M p s p	M. pseudotemporalis profundus

M ps s	M. pseudotemporalis superficialis
M pt d l	M. pterygoideus dorsalis lateralis
M pt d m a	M. pterygoideus dorsalis medialis anterior
M pt d m p	M. pterygoideus dorsalis medialis posterior
M pt r	M. pterygoideus retractor
M pt v l	M. pterygoideus ventralis lateralis
M pt v m	M. pterygoideus ventralis medialis
M r c l	M. rectus capitis lateralis
M r c v	M. rectus capitis ventralis
M s co	M. splenius colli
M se h	M. serpihyoideus
M sp	M. spinalis
M st h	M. stylohyoideus
M th h	M. thyreochoideus
M tr h	M. tracheochoideus
M tr l	M. tracheolateralis
N f h	Nasal-frontal hinge
P ex	Exoccipital process
P i	Internal process of mandible
P r	Retroarticular process of mandible

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